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**Internal Oral Features of
Larvae from Eight Anuran
Families:
Functional, Systematic,
Evolutionary and Ecological
Considerations**

By
Richard Wassersug

UNIVERSITY OF KANSAS
LAWRENCE 1980

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June 24, 1980

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Functional, Systematic, Evolutionary and
Ecological Considerations

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INTRODUCTION

It has been a full century since a biologist first studied tadpole morphology for clues to the evolution and systematics of the Anura (Lataste, 1879). Generally recognized as the most significant work from these last hundred years is that of Orton (1953, 1957), who sorted all frog families into four groups based on larval characters, specifically external oral features and spiracle position.

While herpetologists have largely accepted Orton's four superfamilial groups, there is continual disagreement about relationships between and within these groups. Controversies have centered on the question of how much weight should be given larval characters when larval morphologies suggest relationships different from adult morphologies. Resolution of this question has been hampered by the few larval characters which herpetologists have traditionally considered to have taxonomic value. With consideration of few characters, the chance of convergence is obviously high and confidence in derived systematic relationships is low. Until recently, most work concerning the higher relationships of anurans has involved only a few tadpole external characters. Starrett (1968, 1973) and Sokol (1975, 1977a, 1977b) have now made much progress toward establishing the importance of tadpoles to anuran systematics. Although they have identified many new internal larval features of value to systematic discussions, the larger controversy, unfortunately, has not been resolved. Starrett and Sokol disagree on how to interpret relationships implied by many larval features.

The present study began as a search for additional diagnostic characters to help clarify systematic problems in the Anura (Wassersug, 1976a). It has expanded into a more general, comparative study of the functional morphology and feeding ecology of anuran larvae. An effort is made here not only to identify

characters with systematic import, but to discern patterns in oral features that can be correlated with our knowledge of tadpole ecology.

I present here a comparative study of certain internal oral features of anuran larvae that have not been emphasized by Starrett, Sokol, or other workers. The characters described are all surface features which lie between the opening of the mouth and the esophagus. I have emphasized those organs which come into direct contact with water and food in the mouths of tadpoles and are thus directly involved with the feeding process.

I have chosen to examine morphological structures involved in feeding in part because they are convenient to study. The morphology of tadpoles is dominated by tissue related to feeding functions, especially ingestion, and it seems reasonable to assume that a tadpole's oral morphology will demonstrate adaptation to the environment in which a larva lives. If we understand the adaptive significance of morphological features, we should be able to determine much about the ecology of the tadpole from its oral morphology. An ultimate goal of this comparative study is to understand the morphology of anuran larvae in enough detail to be able to accurately predict a tadpole's ecology from its morphology.

Although this study is limited to surface features, some reference is made to underlying, cartilaginous elements such as the ceratohyal, which forms the piston of the tadpole buccal pump, and the spicule, which supports part of the oral surfaces. A comparative study of the cartilaginous skeleton of the tadpole buccal pump is presented elsewhere (Wassersug and Hoff, 1979).

Only free-living larvae are considered. An ontogenetic series of one species, *Hyla regilla*, was examined in detail in a previous study so that morpho-

logical features modified extensively through development could be eliminated from further consideration (Wassersug, 1976b). It was necessary to do this because not all material available for study is of the same developmental stage.

The core of this paper is descriptions of oral structures in the larvae of selected anuran species. This is followed by a four part Discussion.

The first part of the Discussion (Functional Considerations) reviews the diversity of the structures, and an effort is made here to correlate known larval ecology with patterns in oral morphology. Functions for many of the oral structures presented in the Descriptions are deduced on the basis of what is known about larval ecology. The second part of the Discussion (Systematic Considerations) examines specific systematic questions. The third part (Evolutionary Considerations) deals with questions of evolutionary history as well as the evolutionary mechanisms that could account for diversity among tadpoles. The last part of the Discussion (Ecological Considerations) reverses the first part. Here, starting from a basic understanding of the morphology, an attempt is made to assess the ecology of tadpoles and correlate ecological patterns with known morphological patterns.

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I am extremely grateful to Marsha Greaves, who executed drawings for this paper. Ilse Hecht graciously provided translations of several articles in foreign languages. Shirley Aumiller and Robert Kott helped with photography, portions of the manuscript were typed by Debra Randall and Karen Rosenberg. Special thanks are due Nancy Bradney, who helped in many aspects of production and editing. Steve Busack, William Duellman, Robert Inger, Dianne Seale, Otto Sokol, Linda Trueb and David Wake have read various portions of this manuscript; it has profited greatly from their constructive criticisms.

MATERIALS

Oral structures of larvae of 31 species from eight families are described. The tadpoles came from museum collections or the author's private collection. An effort was made to examine specimens at or near Gosner (1960) stage 36.

A few species (e.g. *Acris crepitans*) were chosen for study because they have the commonest type of anuran larvae (i.e., denticle pattern 2/3; inhabitants of small ponds and pools) and serve as reference forms for comparison with tadpoles of more exotic morphologies and ecologies. All other species were selected

either because they came from families whose larvae have been associated with interesting taxonomic problems or because they present unusual larval ecologies. Particular emphasis was placed on the frogs assigned to the superorder Archaeobatrachia by Duellman (1975); thus *Ascaphus* (Ascaphidae), *Alytes*, *Bombina*, *Discoglossus* (Discoglossidae), *Rhinophrynus* (Rhinophrynidae), and several pelobatid larvae are described. Since the Microhylidae is a family of particularly problematic relationships, several *Microhyla* larvae are also described.

Hylidae larvae were selected because of their great ecological diversity (see Duellman, 1970) while one member of the Centrolenidae and two species of Dendrobatidae are described solely because of their unusual larval ecology.

Certain families are not treated here because species from these families have been described or illustrated elsewhere: for example Pipidae (Sokol, 1975, 1977a and other references cited therein); Ranidae [*Rana agilis* (Kratochwill, 1933), *Rana temporaria* (Savage, 1952; DeJongh, 1968), *Rana catesbeiana* (Gradwell, 1970, 1972a), *Rana fuscigula* (Gradwell, 1972c)], and the Pseudidae (*Pseudis paradoxa* larvae illustrated by W. Parker, 1881). One bufonid, *Bufo bufo*, has been partially described and illustrated by Savage, 1952. The availability of specimens set some constraint on the families that could be studied; several major families with tropical distributions (e.g., Leptodactylidae and Hyperoliidae) are left for future work.

Knowledge of the habitats and feeding ecology of the larvae studied here is summarized below. The species are

loosely grouped by common features either of external morphology or ecology (references for most of these comments are given in the descriptions).

BENTHIC LARVAE WITH ENLARGED SUCTORIAL MOUTHS

ASCAPHIDAE.—*Ascaphus truei*: adhere to rocks in streams; well known for their large suctorial oral disc and adaptation to torrential habitats.

PELOPATIDAE. — *Leptobrachium hasselti*: inhabit quiet, clear regions of streams, where they graze on algae growing on rocks. In terms of body shape or tail length, *L. hasselti* larvae are little specialized for stream life, and are among the more generalized megophrynine tadpoles. *Leptobrachium oshanensis*: more specialized to stream life than *L. hasselti* (Liu, 1950:191-201) since larvae have very long, strong tails and are good swimmers in running water; they stay on the bottom in shallow water and have an expanded oral disc, with a large denticle-free area.¹ *Oreolalax pingii*: similar to *Leptobrachium* larvae in general appearance; described as "bottom feeders" (Liu, 1950). Their morphology suggests that they are intermediate in their tolerance for currents between *L. hasselti* and *L. oshanensis*.

HYLIDAE.—*Hyla mixe*: among the most highly specialized larvae for stream life; have very large oral disc used for adhering to rocks in strong currents. *Ptychohyla leonhardschultzei*: inhabit small, quiet, peripheral pools in mountain streams. *Smilisca sordida*: inhabit streams, but only in regions of very gentle current; externally, they show few of the modifications characteristic of stream tadpoles.

¹ Liu (1950:200) questioned the common interpretation (after Smith, 1926) that the mouth serves an adhesive function. He watched an *L. oshanensis* larva in his laboratory and noticed that when it rested on the bottom, only the tips of the marginal papillae touched the substrate. Water flowed into the mouth through the notch at the front and the back of the disc. Liu then concluded that the oral disc served the function of raising the head off the bottom to allow for respiration. His observations, however, remain inconclusive for the natural situation, because he described the action of the disc only in tadpoles confined to quiet water. The disc may still have an adhesive function in currents, not only for this species, but for all other species with enlarged oral discs.

FUNNEL-MOUTHED TADPOLES

MICROHYLIDAE.—*Microhyla heymonsi*: inhabit quiet pools and feed on particles at the air-water interface; have rapidly vibrating, filamentous tail tip and can remain seemingly motionless at the surface film for long periods of time.

PELOBATIDAE.—*Megophrys minor*: epitomize the surface film-feeding way of life; have a huge, upwardly directed, denticle-free oral disc;² occur in slow, flowing water and are, consequently, equipped with a long, powerful tail which allows them to resist displacement downstream.

HYLIDAE.—*Ptychohyla schmidtorum*: moderately specialized for stream existence; found in the quieter reaches of mountain pools; have expanded oral discs with a large denticle-free area.

DENDROBATIDAE. — *Colostethus nubicola*: In aquaria they swim beneath the surface film (Savage, 1968). They have a large, anterior-directed oral disc with surface papillae which, according to Savage, aid in sorting particles from the water. Found under vegetation and rocks in side pools and rivulets of small streams; found in pools sufficiently small so as to be occupied rarely by fish.

"FOSSORIAL" STREAM FORMS

CENTROLENIDAE.—*Centrolenella fleischmanni*: extremely elongated larvae which lack the suctorial mouth or funnel of other stream forms; found in cracks and crevices amongst the rocks and vegetation in shallow streams.

HYLIDAE, Arboreal Larvae.—*Anothea spinosa*: live in the shallow water that collects in tree holes; known carnivores with large beaks; specialized for feeding on mosquito larvae, other arthropods, and frogs' eggs. *Hyla dendroscarta*: extremely elongated tadpoles which live burrowed in the leaf axils of

bromeliads; macrophagous (according to Orton, 1944) but lack the large mouth of *Anothea spinosa* and presumably are more dietary generalists, feeding on small fragments of animal and plant matter that collect in their arboreal pond.

MIDWATER MACROPHAGOUS LARVAE

MICROHYLIDAE.—*Microhyla berdmorei*: dispersed throughout the water column in quiet pools; lack keratinized mouth parts and are obligate feeders on fine, suspended matter. *Microhyla ornata*: found suspended throughout the water column; presumably similar in their feeding habits to *M. berdmorei*.

HYLIDAE.—*Agalychnis callidryas*: by rapidly vibrating the pointed tips of their tails these larvae can hang suspended in midwater in ponds; retain the typical hylid 2/3 denticle pattern and can facultatively graze on substrates besides feeding on microscopic particles midwater (see pers. comm. by McDiarmid in Heyer, 1976:22).

TEMPORARY POOL DWELLERS, Omnivores

RHINOPHRYNIDAE. — *Rhinophrynus dorsalis*: larvae lack keratinized mouth parts for biting or scraping, but are omnivores able to cannibalize smaller individuals and also efficient suspension feeders of ultraplanktonic particles.

PELOBATIDAE.—*Scaphiopus bomifrons*: active tadpole found in temporary pools and known for rapid development and voracious feeding habits. Although carnivorous and cannibalistic, best considered omnivores; an oral disc of moderate size surrounding large and powerful beak; members of genus are efficient suspension feeders (Richmond, 1947).

ADDITIONAL POND LARVAE

DISCOGLOSSIDAE.—*Alytes obste-*

² According to Liu (1950:191) the disc folds shut when the tadpole is below the surface, but opens to form a funnel at the surface film when the tadpoles are feeding. The funnel may function in both feeding and respiration as a surface float; literature on the subject has been reviewed by Noble (1927) and Liu (1950).

tricans: typical for quiet water tadpoles in general appearance and behavior; able to stay in midwater by gulping air intermittently, but feed on vegetation at or near the bottom. *Alytes cisternasii*: presumably similar to *A. obstetricans*. *Bombina orientalis*: occur in assorted ponds or pools, often adjacent to streams; can be found in puddles lacking macroscopic vegetation; can be carnivorous. Perhaps appropriately viewed as omnivores with generalized external structures, capable of carnivory and suspension-feeding on microscopic particles. *Discoglossus pictus*: generalized pond larvae, presumably similar to *Alytes* and *Bombina*.

HYLIDAE.—*Gastrotheca riobambae*: inhabit shallow, high elevation pools and exhibit no unusual behavior for anuran larvae. *Hyla femoralis*: midwater forms that live amongst vegetation in pools; have exceptionally high tail fin with terminal filament, but otherwise "typical" in their external morphology and feeding habits. *Hyla rufitela*: live in small pools, often overgrown with macrophytes; have an unusual 2/4 denticle pattern but not known to have unusual feeding ecology. *Hyla ebraccata* and *Hyla sarayacuensis*: hide among the aquatic plants of the shallow parts of ponds, where the adults of the species breed; larvae characterized by a reduction of the oral disc and the loss of denticle rows as compared with typical pond hylids; members of species group feed on submerged leaves or other debris (Starrett, 1973). *Hyla phlebodes*: found among vegetation in shallower parts of pools; have small mouth without oral disc and denticle rows; members of species group feed on the bottom (Starrett, 1973). *Acris crepitans*: typical generalist tadpole of small ponds and pools throughout much of eastern United States. *Colostethus nubicola*: inhabits

small, rocky ponds; details of feeding ecology unknown.

METHODS

All tadpoles examined were measured from snout to vent and staged according to Gosner, 1960. For each tadpole the floor and the roof of the mouth were exposed following a simple dissection procedure described by Wassersug (1976a). Tadpoles were pinned under water in a small tray of darkly stained paraffin and examined with a dissecting microscope. The larvae were lightly stained with either methyl blue or crystal violet to accentuate surface features, specifically mucous-secreting epithelia.

Ventral and dorsal surfaces were photographed on 4" × 5" format through a bellows-view camera using a 32 mm lens; a few photographs were taken with 16 or 64 mm lenses. Tadpoles were usually pinned to the paraffin at the tail only; care was taken not to distort or stretch oral surfaces. Camera lucida drawings were also made of many of the specimens, particularly the smaller ones. Either camera lucida drawings or photographs accompany the descriptions for most species; some descriptions have both for purposes of comparison. One species is described without photograph or illustration because it is nearly identical to related forms that are illustrated.

All illustrations in this descriptive section present the buccal floor and buccal roof as a single plate with the floor above and roof below; for drawings, dorsal and ventral surfaces are magnified equally and a single scale line (=1 mm) is given. For the photographs, a single scale line is given if both halves of the plate are magnified equally; otherwise two separate scale lines are used.

Just as there are optical limits on photomicrographical qualities,³ there are hu-

³ An effort was made to obtain scanning electron (SEM) photomicrographs of several small specimens because of the potential resolution and depth of field provided by this technique. SEM, however, had to be abandoned because it required pre-coating the specimens with a uniform, conductive metallic layer and the convoluted, intricate structure of the gill filters made such preparation impossible.

man limits on how accurately certain ventral, pharyngeal features—specifically, the gill filters—can be drawn. The gill filters in many of the drawings are slightly stylized; minor discrepancies between the descriptions and the drawings remain.

Species descriptions are grouped by family. Each description is provided with a reference or references that pertain(s) to the species morphology, ecology, or both. The morphological descriptions follow Wassersug (1976a). Meristic features are presented for both the left and right sides of the buccal roof and floor; discrepancies between one side and the other, are noted. These data, which were originally collected to determine whether asymmetries in external aspects of the respiratory system (i.e., position of the spiracle) were reflected internally, give some indication of the amount of variation in any species. Meristic data from the pharynx are all taken from the left side. It can be noted

here that no consistent pattern of left or right handedness was found, either intraspecifically (for *Hyla regilla*; Wassersug, 1976b) or interspecifically.

Because of the complex, qualitative nature of many of the features described, I chose not to use a telegraphic form for the descriptive body of the study. *Hyla regilla*, illustrated and described in detail in Wassersug (1976b), is treated as the “typical” pond tadpole and considered a reference for comparison with the other forms.

Figures 1 and 2 show nearly all structures presented in the species descriptions. All morphological structures described are briefly defined in the Glossary. Terminology follows Wassersug (1976a).

Two sources are followed for anuran systematics. I follow Orton (1957) in recognizing four larval types. Type 1 includes the Pipidae and the Rhinophrynidae; Type 2 consists of the Micro-

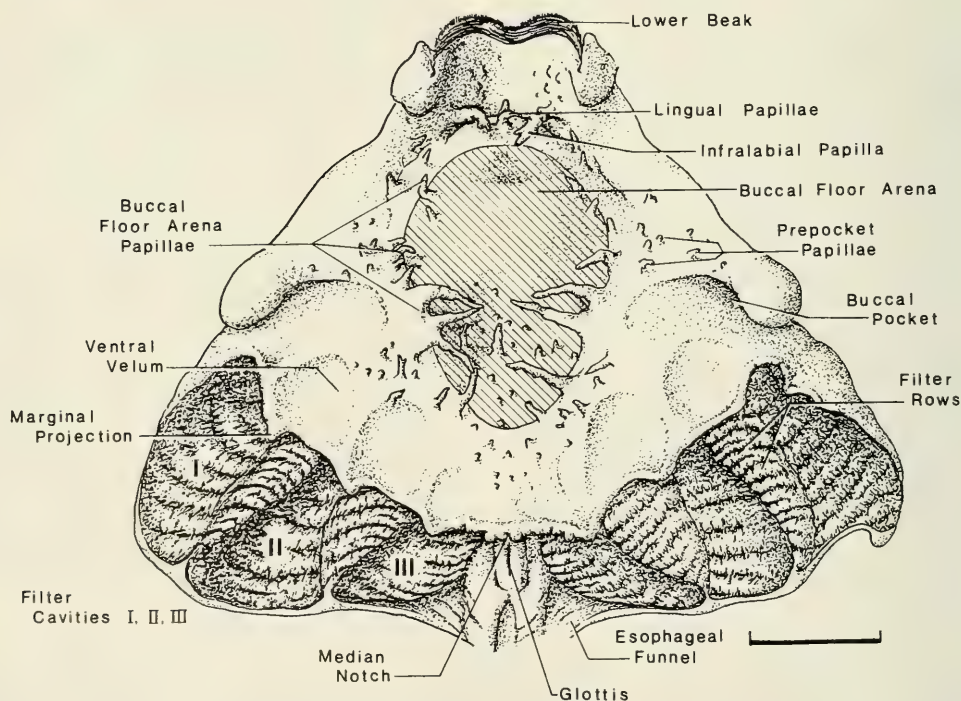


FIG. 1.—The floor of the mouth in a *Hyla femoralis* larva. Most morphological features discussed in the text are labelled in this Figure and Fig. 2. The scale line equals 1 mm.

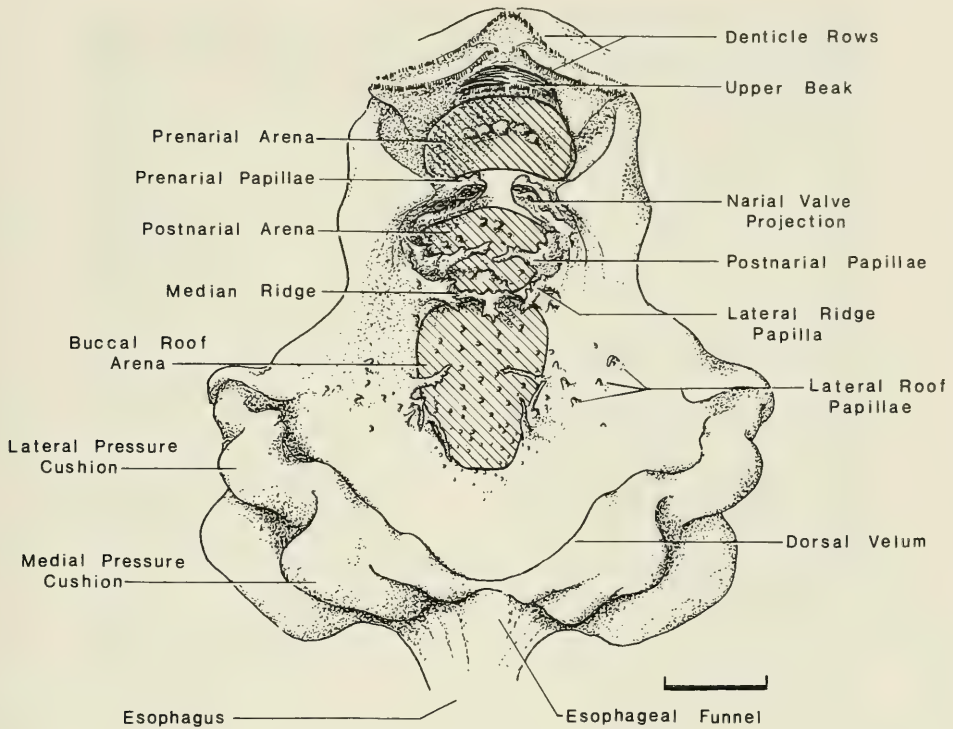


FIG. 2.—The roof of the mouth in a *Hyla femoralis* larva. Most of the morphological features discussed in the text are labelled in this Figure or the previous one. The scale line equals 1 mm.

hylidae only; Type 3 includes the Ascaphidae and Discoglossidae; and Type 4 includes all the remaining families. Starrett (1973) has given formal names to these groups. As I am not convinced that this series represents a phylogenetic sequence, I am reluctant to follow Starrett's names. Unless otherwise noted I follow Duellman (1975) for the basic

taxonomy of the Anura and recognize two broad groups of frogs, the archaic (Archaeobatrachia) and advanced (Neobatrachia) forms. Which families belong to which group is highly controversial (cf. Sokol, 1977b) and I deal with this question to some extent in the discussion sections on systematics and evolution.

DESCRIPTIONS

ASCAPHIDAE

Ascaphus truei Stejneger

(Fig. 3)

Material.—FMNH 166497 (stage 37, sv. 18.0 mm). Bird Tributary to St. Joe River, Shoshone Co., Idaho, U.S.A.; July 22, 1965.

Reference.—Stebbins, 1951 (p. 192).

External.—*Ascaphus truei* larvae have a large suctorial oral disc, and a medial spiracle. This description is

based on a typical individual with a 3/11 denticle pattern, of which two upper and three lower rows were multiple.

Ventral buccal.—The floor of the oral cavity is slightly expanded anterolaterally; bilateral infralabial papillae are absent. Immediately inside the mouth is a single flap-like fold of skin identifiable as a posteriorly-directed, bilobed, oral valve, the free edge of which supports nine very small evenly spaced papillae. The tongue, a transversely elon-

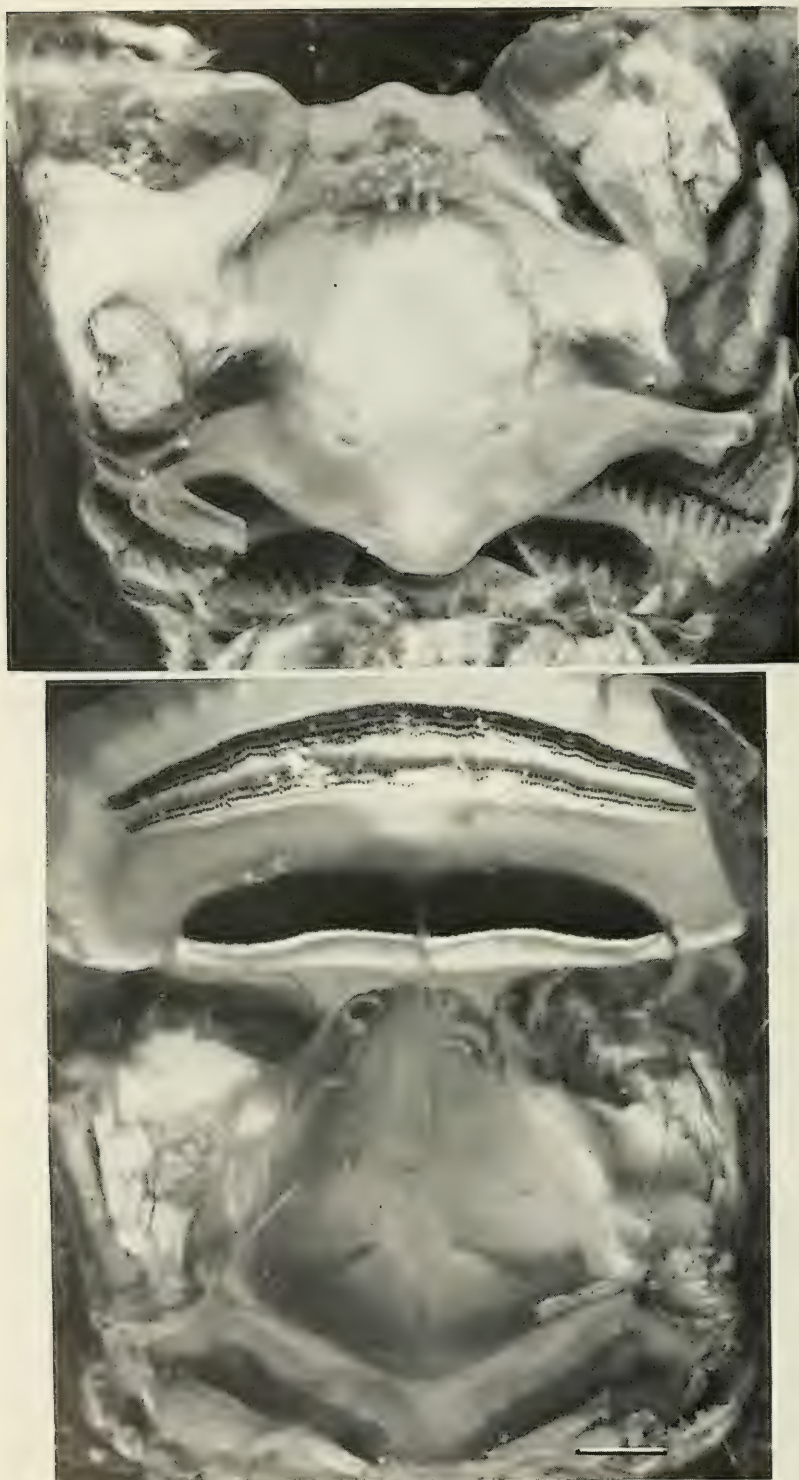


FIG. 3.—Photographs of the floor (above) and roof (below) of the mouth in an *Ascapthus truei* larva. The scale line in this Figure and all that follow equals 1 mm.

gate dome, is covered with a dense field of several dozen, straight, blunt papillae. The majority of these lingual papillae are tall and subequal in size, but the anterior ones are smaller and thinner than the rest. The BFA papillae are organized in a broad, V-shaped row that begins anterolaterally as prepocket papillae. The BFA papillae are eight per side, simple, straight and of modest size. They become progressively smaller posteromedially. Pustulations and papillae of any sort are absent from the remainder of the buccal floor. Buccal pockets are long and shallow and unperforated. The free velar surface is comparatively short. Its posterior margin is shaped like a very broad "V" with a curved apex and it lacks posterior projections or a median notch. The velar margin forms a rim twice as thick as the free velar surface in front of it. The margin is curved upward; directed dorsal rather than caudad. It is stiff, but no spicule support is evident; its rigidity results in part from the complete anchoring of the ventral velum to the dorsal margin of the filter plate on cb. 2. In fact, the velar surface extends posteriorly in thin, tapered bands for half the length of these filter plates. Well-formed secretory pits could not be resolved, however, the velar margin is covered densely with extremely small, fine, irregular pittings. The anterior limits of this unusual mucosa could not be determined.

Ventral pharynx.—The pharynx in *Ascaphus truei* is overall proportionally as large as in typical pond tadpoles, but the filter plates are rotated outward so that cb. 2 is more transversely oriented and filter cavity 3 is reduced in volume on each side. Filter plates of cb. 2 are straight while those of cb. 3 are strongly bowed, obscuring much of filter cavity 3 from dorsal view. Counts for number of filter rows on cb. 1-4 are 9, 11, 10, 6 respectively. The filter mesh of *A. truei* is much reduced. Secondary filter folds are short; tertiary folds are short and

few. Neighboring filter rows do not abut, so filter canals are large, open channels, almost as wide as the filter row. The branchial food traps are small but well demarcated ventrally, where a sharp rim separates them from the filter tissue. Secretory ridges could not be resolved and must be extremely fine or absent. The glottis is a tiny, unperforated slit under the velar margin. Glottal lips and a conspicuous laryngeal disc are absent. The esophageal funnel has a narrow dorsal profile.

Dorsal buccal.—The buccal roof is dwarfed in comparison to the huge upper beak, and much narrowed anteriorly. The roof is transversely arched and has considerable depth compared to other species. The oral opening is small and positioned so far posterior that the pre-narial arena is also "preoral." The arena is a slim, blind tunnel above the upper beak. It is devoid of papillae or pustulations. The internal nares are oblique, nearly longitudinally oriented slits and are on the lateral walls rather than on the roof of the buccal cavity. The anterior narial walls make an anterolateral loop that bounds small, oval, oblique pits on each side. The walls surrounding these pits are thick and pustulate. The remainder of the anterior walls are shallow and lack papillae. The posterior narial walls are tall and slightly pustulate, but lack narial valve projections. All major landmarks of the buccal roof proper, such as the median ridge and papillae that could outline the post-narial and buccal roof arenas, are absent. There are approximately ten small, simple, blunt papillae scattered about the buccal roof behind the nares; these show some tendency to be concentrated in the posterolateral corners of the buccal roof. The buccal roof sinks, then rises again just anterior to the dorsal velum, and forms a major, posteriorly directed V-shaped depression. The anterior surface of this depression is lined with a few blunt, well-spaced pustulations. The glandular zone begins at the

lowest point of this depression. The zone is of uniform anterior-posterior length except directly in front of the esophagus, where it is much abbreviated. The zone is made up of irregularly spaced, minuscule secretory pits that are extremely dense. The dorsal velum is short and thick with a smooth ventral margin. It is continuous across the midline, but its full extent in that region cannot be determined because of damage in dissection.

Dorsal pharynx.—The two pairs of pressure cushions in *A. truei* are of typical size and dimension. They are, however, covered with a few faint, scattered pustulations along with a dense secretory epithelium. The ciliary groove is broad and shallow.

Diagnostic summary.—The oral cavity of *Ascaphus truei* differs from that of all other tadpoles examined in the following, unique characters: presence of oral valve instead of paired infralabial papillae; many papillae covering tongue anlage; prenarial arena reduced to short, blind tunnel; sensory pits anterolaterally on the internal nares; large V-shaped depression extending across posterior buccal roof. A combination of the following features further differentiates the oral cavity of *Ascaphus* larvae from all other tadpoles: ventral velum fully attached to dorsal margin of filter plates; secretory tissue without pitted or ridged pattern; unperforated glottis; absence of prenarial, postnarial and buccal roof arenas.

DISCOGLOSSIDAE

Alytes obstetricans Laurenti

(Figs. 4, 5)

Material.—Uncatalogued, author's collection (stage 36, sv. 18.5 mm). Collected at "La barlieu," 30 km SE of Lyon, Rhône, France; no date.

References.—Eibl-Eibesfeldt, 1953; Magnin, 1959.

External.—*Alytes obstetricans* tadpoles have a 2/3 denticle pattern with

the inner upper and two inner lower rows multiple. The spiracle is medial.

Ventral buccal.—The floor of the oral cavity is relatively wide anteriorly and rounded rather than pointed. The buccal floor is flat but slopes forward so that the frontal plane of the mouth meets the frontal plane of the trunk at an angle; these planes are more nearly parallel in most tadpoles. Infralabial papillae are tall, narrow and have a fine serrated margin rather than secondary papillae. The transversely elongate tongue anlage lacks lingual papillae but is covered fully by a dense field of stout, blunt pustulations. The buccal floor arena is surrounded by eight BFA papillae on one side and ten on the other. These BFA papillae are less numerous in front of the buccal pockets, more numerous posteriorly and slightly more attenuate and acutely pointed when compared to those of typical pond tadpoles. A couple of the largest papillae are laterally compressed and have terminal bifurcations. There are two distinct conical prepocket papillae on each side. Some extremely tiny, pointed papillae are clustered directly anterior to cb. 2 on the buccal floor, and there is a single small papilla above the lateral arm of the ceratohyal on each side in this specimen. Dozens of tiny, precise pustulations cover the buccal floor, with their greatest concentration anterolateral and posteromedial. Each buccal pocket has a large transverse pouch with a heavy fold rising off its posterior wall obscuring its floor. No open slit could be found within the pockets. The free velar surface is reduced. Spicular support is lacking except for a tiny spur of cartilage at the points where the dorsal edge of the filter plates on cb. 3 meet the velum. The velar margin is fully fused to the top of the filter plates on cb. 2 and fused almost to its edge above cb. 3. The velum edge is curved upward above cb. 2. The velar margin is concave posteriorly between filter plates and when viewed from above appears

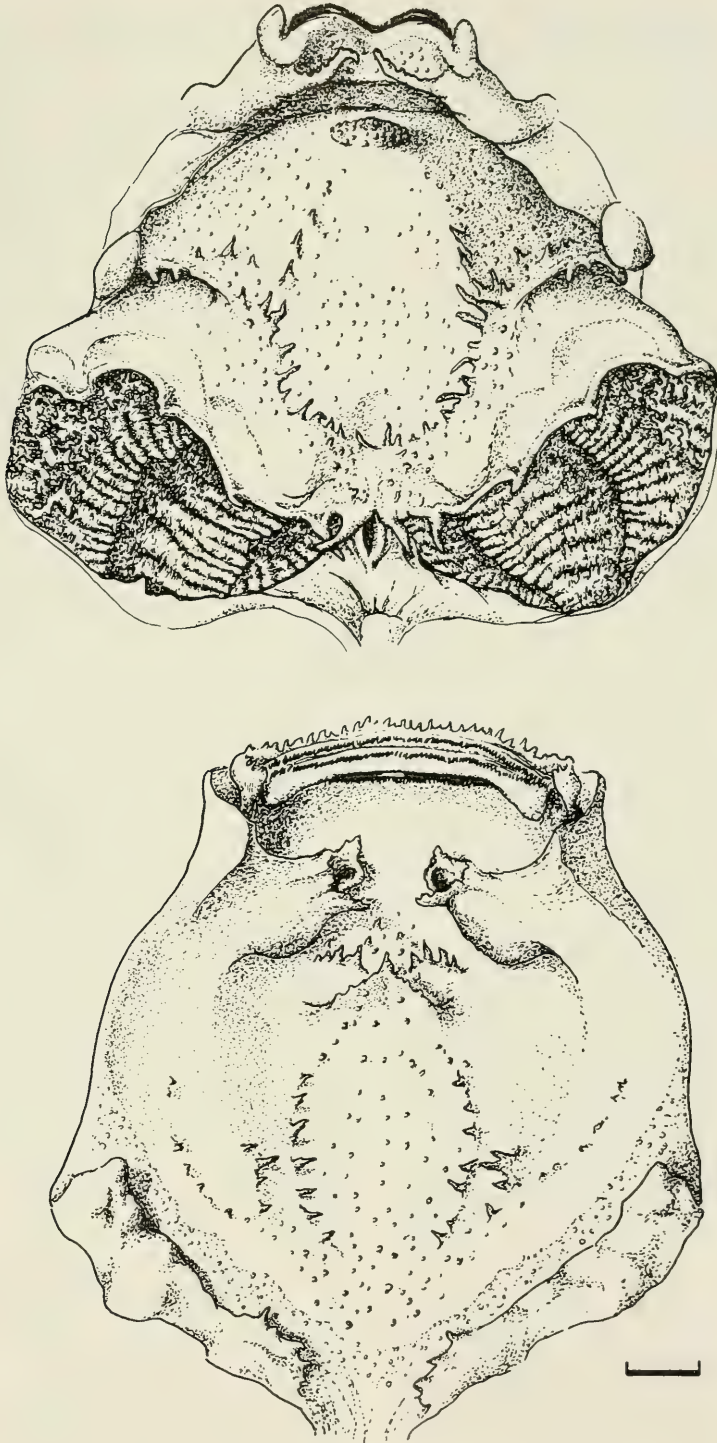


FIG. 4.—Drawings of the floor (above) and roof (below) of the mouth in an *Alytes obstetricans* larva.

as a series of crescents rather than a continuous posteriorly convex arc. Projections of the velar margin are displaced medially and are pointed rather than curved. The projections associated with the third filter cavity and the medial notch are long, finger-like papillae. Secretory pits are restricted to the posterior projections of the velar margin. The pits are small and of low density.

Ventral pharynx.—The branchial baskets of *A. obstetricans* are round, long, wide and deep. The first and second filter cavities are disproportionately large compared to the third. The dorsal margins of the filter plates of cb. 3 arch upward and blanket much of the third filter cavity. Although the filter plates are relatively long in *A. obstetricans*, the number of filter rows and density of the filter mesh is low. Counts for filter rows are 6, 9, 8, 5, for cb. 1-4. The filter mesh is comparatively reduced because the rows are narrow, and secondary and tertiary filter folds, while present, are very thin. The filter canals are large, nearly fully open channels. The short, flexible surface of the velum is covered ventrally by small, scattered secretory pits rather than by secretory ridges. These pits grade into weak "ridges" farther forward under the immobile portion of the velum. The "ridges," however, are not well-formed and have a rather streaked appearance. The area covered by the secretory tissue is rather small and sharply separated from the filter epithelium by a rim around the food traps in each filter cavity. The glottis is 90% visible from above. It is long with large thick lips. The laryngeal disc, however, is not exceptionally large. The esophageal funnel is large and broad in dorsal profile.

Dorsal buccal.—The buccal roof is broad anteriorly and has a "V" shaped posterior pharyngeal margin. The pre-narial arena is as large as that of the typical pond hylids examined, but appears shorter in photographs because it is partially obscured by a posterior re-

flexion of the upper labial cartilage and beak. The pre-narial arena is devoid of any papillae, pustulations, ridges or other projections. The internal nares of *A. obstetricans* are elongate, obliquely oriented slits. Their anterior walls each have a low, tiny, anteriorly-directed flap at their most anteromedial corners. Normal pre-narial papillae are absent, however; the anterior narial walls abruptly expand into huge flaps that extend back the length of the nares. These flaps curl posteromedially under the narial openings. The tall, anteromedial edges of these flaps are serrated. The coiled, posterior margins of the flaps have a few small, pointed, irregular secondary papillae on each side. The posterior narial walls have valves but lack any narial valve projections. Eight small, pointed cones of subequal size make up the post-narial papillae series. These papillae are clustered in a rather transverse patch in the middle of the post-narial arena. The median ridge is an anteriorly directed, triangular flap. The anterior surface of the median ridge is smooth but two tiny cusps line the lateral margins of the ridge on each side. Separate lateral ridge papillae are absent. The BRA is an elongate oval defined by approximately six, well-spaced papillae on one side and five on the other in this specimen. The BRA papillae are all small, pointed cones of subequal size. In addition to the main rows of papillae, there are two single papillae lateral to the arena on each side and an arc of tiny conical papillae at the posterolateral margins of the buccal roof. Randomly dispersed within the BRA are 50-60 tiny pustulations. Pustulations are absent outside of the arena. The glandular zone is normal. The dorsal velum is short and not tightly coiled. It is completely and broadly interrupted medially and its medial edges are papillate on each side.

Dorsal pharynx.—Although two broad, shallow waves of the velar surface are faintly visible in this specimen, pressure cushions are essentially absent.



FIG. 5.—Photographs of the floor (above) and roof (below) of the mouth in an *Alytes obstetricans* larva.

The ciliary groove is similar to or slightly broader than that of a typical pond larvae.

Diagnostic summary.—Tadpoles of the family Discoglossidae can be distinguished from those of all other families by the presence of large flaps of the anterior narial walls which curl posteriorly under the nares and their V-shaped posterior pharyngeal margin. All discoglossid tadpoles have the posterior, ventral velar margin ankylosed to the dorsal margins of the filter plates and appear to lack well organized secretory ridges in the branchial food traps. Internally *Alytes* tadpoles differ from other discoglossid larvae in the presence of four long projections of the ventral velum near the midline and pustulations covering the tongue anlage. Compared to *A. cisternasii*, *A. obstetricans* tadpoles lack paired lingual papillae, but have an oval-shaped buccal floor arena, shorter, fewer BFA papillae and slightly denser gill filters. *A. cisternasii* larvae tend to have more papillate and crenulated structures than the larvae of *A. obstetricans*; this can be seen in the infralabial papillae, the narial flaps and the median ridge. *A. obstetricans*, however, is the only discoglossid examined with papillation of the median edge of the dorsal velum.

Alytes cisternasii Bosca
(Fig. 6)

Material.—Author's collection (stage 34; sv. 15.5 mm). Collected in a permanently swampy area, in the province of Alto Alentejo, Portugal; no date.

Reference.—Boulenger, 1891.

External.—*Alytes cisternasii* have large robust larvae which in terms of size, shape and denticle pattern are virtually identical to *A. obstetricans*. The spiracle is medial. Boulenger (1891) could detect no characters that distinguish the larvae of these two species but Crespo (pers. comm.) finds that in Portugal *A. cisternasii* larvae have a larger spiracle with a shorter, free terminal

sleeve and generally fewer denticles than *A. obstetricans* larvae. The specimen described here had a 2/3 denticle pattern with all rows multiple.

Ventral buccal.—(Unless otherwise noted *A. cisternasii* is identical to *A. obstetricans*). *A. cisternasii* has several pustulations inside the oral orifice anterior to the infralabial papillae. Among the pustulations on the tongue anlage, two near the midline are particularly enlarged and, as such, resemble in shape and position the typical paired lingual papillae of most anuran larvae. Buccal floor arena papillae are taller and more numerous in this species. I count nine major papillae on one side, twelve on the other with an equal number of minor papillae as well as many small pointed pustulations in the posterior part of the arena and interspersed among the papillae forming the margins of the arena. There are several small conical papillae in front of the pockets on each side. Papillae posterior to the BFA are lacking. There appears to be less spicular support than in *A. obstetricans*. Single secretory pits could not be discerned even at 100 \times .

Ventral Pharynx.—The branchial baskets are slightly more triangular in dorsal view than those of *A. obstetricans* and perhaps a bit smaller in comparison to the size of the buccal cavity overall. Counts for filter rows run 9, 10, 8, and 5 for cb. 1-4 respectively, which means that for individuals of comparable size and stage *A. cisternasii* has slightly more filters rows than *A. obstetricans*. In contrast, filter mesh appears slightly denser than in *A. obstetricans* but this difference may be due to preservation. The filter canals are necessarily less open in this specimen than in the specimen of *A. obstetricans* described above. No secretory ridges were evident in the branchial food traps. The glottis is less than 50% visible from above. The glottal lips are not as thick as in *A. obstetricans*.

Dorsal buccal.—The flaps at the anteromedial corners of internal nares in

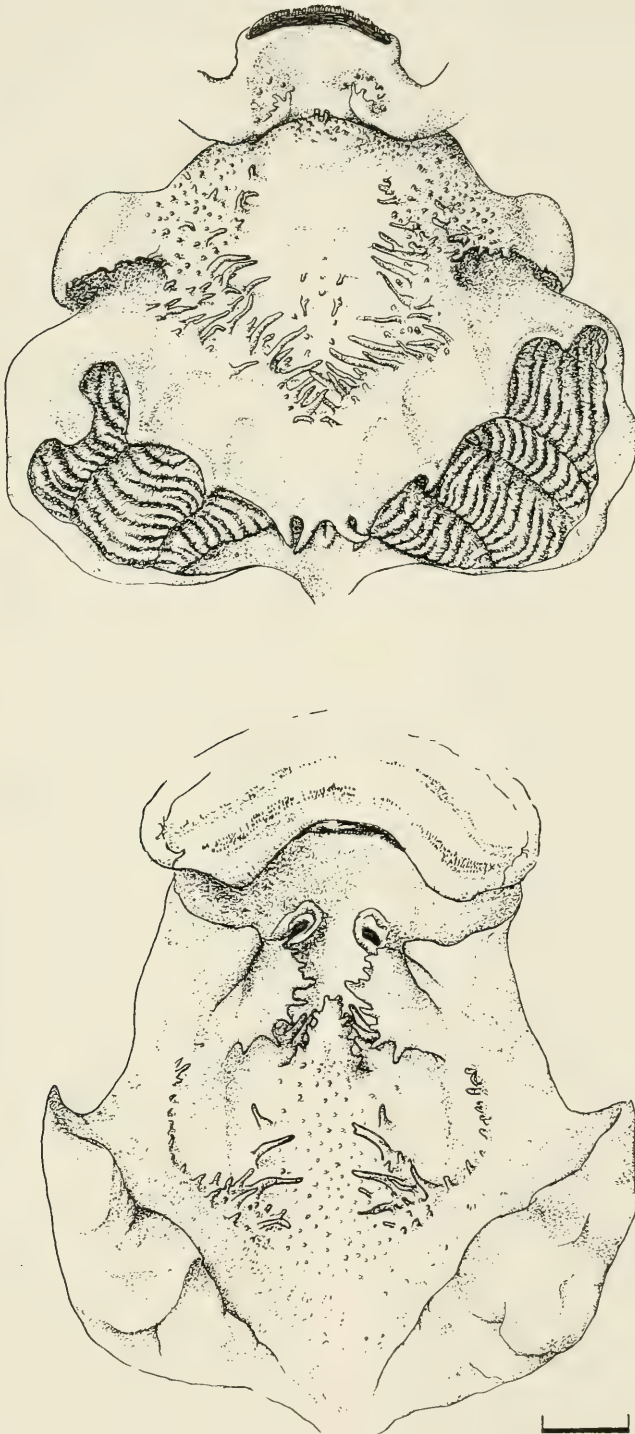


FIG. 6.—Drawings of the floor (above) and roof (below) of the mouth of an *Alytes cisternasii* larva.

A. obstetricans are present in this species but much reduced. The large postero-medially directed flaps that arise from the anterior margin of the narial walls have a more distinctly papillate margin in this species compared with *A. obstetricans*. There are nine pointed cones within the postnarial arena. The median ridge in this species has a more crenulate border than in *A. obstetricans*. The BRA is defined by approximately seven papillae on one side and five on the other in this specimen. The BRA papillae are more attenuate overall. The medial edges of the dorsal velum lack papillae but are pustulate in this specimen. Most other differences illustrated in Figs. 4 and 6 reflect differences in dissection.

Dorsal pharynx.—As in *A. obstetricans*.

Diagnostic summary.—See *Alytes obstetricans* (p. 14).

Bombina orientalis Boulenger
(Fig. 7)

Material.—Uncatalogued, author's collection (stage 34, sv. 14.1 mm). Laboratory raised population, Amphibian Facility, University of Michigan, Ann Arbor, Michigan. Initial stock from Korea with no additional data.

Reference.—Okada, 1931.

External.—*Bombina orientalis* larvae have a 2/3 denticle pattern with the inner rows double. The spiracle is medial, characteristic of discoglossid tadpoles.

Ventral buccal.—The floor of the mouth of *B. orientalis* is proportionally longer than that of *A. obstetricans* with the increase solely in the pharynx. As in *A. obstetricans*, the floor tips anteriorly downward from the frontal plane of the trunk. The mouth is anteriorly narrower than in *A. obstetricans*. A single, strongly compressed, dorsally projecting infralabial papilla is situated on each side in the typical position. These are not as tall as in *A. obstetricans*. Anteriorly, the papillae grade into a series of pustulations that are continuous across the mid-

line. Posteriorly, the papillae degenerate into a jagged fringe. The free edges of the infralabial papillae are lined with short, attenuate, secondary papillae, eight on each side in this specimen. The single, median lingual papilla, situated far anterior, is anteriorly to posteriorly flattened and slightly concave posterad. It has a deep median notch and small, secondary, terminal subpapillate projections. Posterolaterally on each side of the tongue anlage are single, large, conical pustulations. The papillae of the BFA are much reduced in size and aligned in a "V" with the arms of the "V" forward. Anteriorly each arm turns laterally so the BFA papillae series is continuous with the prepocket papillate series. I counted six BFA papillae on one side and seven on the other, with an additional three papillae on each side in the prepocket papillae position. The prepocket papillae and the largest BFA papilla on each side have fine secondary, pointed, terminal papillae. Other papillae in the BFA row are simple, small, laterally compressed cones that grade down to pustulations. There are a few tiny pustulations near the prepocket papillae, but the remainder of the buccal floor is smooth and free of any additional papillae or pustulations. The buccal pockets are unperforated and have the same orientation and length to width ratio as in *A. obstetricans*. They are, however, shallower. The short, free velar surface lacks spicular support but is quite inflexible due, in part, to the fact that it is fused almost to its margin at the top of the filter plate of cb. 2. The velar margin is posteriorly concave between filter plates, giving the free velar surfaces the appearance of a series of crescents as in *A. obstetricans*. These projections are directly above the filter plates. The median portion of the velum forms a discreet series of waves and lacks a large median notch. The edge of the velum is curled up to form a thickened rim continuous from one side to the other similar to, but not as large as, the

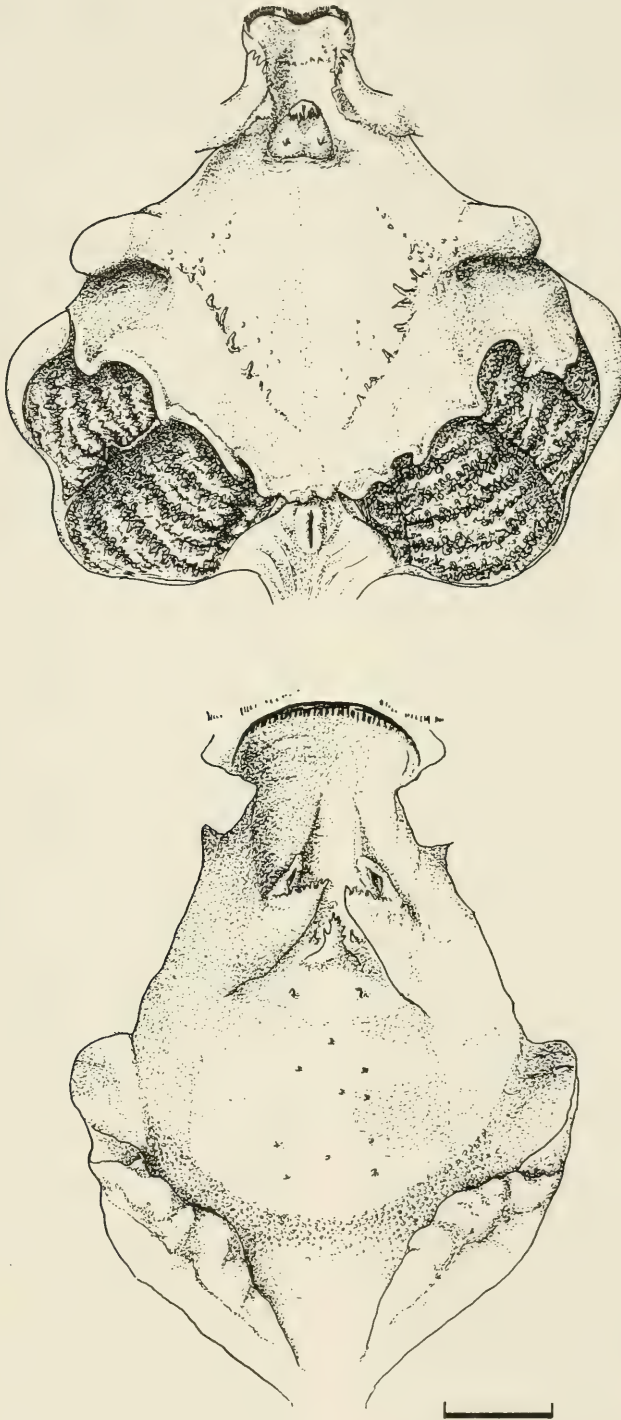


FIG. 7.—Drawings of the floor (above) and roof (below) of the mouth of a *Bombina orientalis* larva.

raised velar margin in *Ascapthus truei*. The rim has the buffed texture characteristic of secretory tissue but distinct secretory pits could not be resolved.

Ventral pharynx.—The branchial baskets are slightly taller and longer than those of *A. obstetricans* and much taller and longer than those of typical pond tadpoles. They are tallest posterolaterally, where they extend well above the plane of the floor of the mouth. Compared with *A. obstetricans*, the third filter cavities of *B. orientalis* show further reduction in volume at the expense of larger second filter cavities. The filter plates, particularly those of cb. 3, are imbricated to a great extent in *B. orientalis*. Counts for numbers of filter rows run 8-9, 11, 10, 6 for cb. 1-4. The filter mesh is similar to that of *A. obstetricans*. Filter rows are unusual in being very uniform in thickness and little expanded ventrally. The main fold is very straight and second folds are single, short crossbars on the main fold. Filter rows do not abut and the filter canals are large, open channels. Branchial food traps are extremely short and separated from the filter surfaces ventrally by a large, distinct rim. Secretory ridges could not be resolved anywhere in the food traps even at $75\times$. They are presumably absent; nevertheless, the food traps are covered with a buff-textured tissue that has the superficial characteristics of a glandular mucosa. The glottis of *B. orientalis* is larger than that of typical pond tadpoles, but smaller than that of *A. obstetricans*. The glottal lips are thickest in *B. orientalis*. The laryngeal disc is present, but not very distinctive. Fifty percent of the glottis is obscured from dorsal view by the margin of the velum. The esophageal funnel has a narrow profile. The bore of the esophageal funnel, however, is large in *B. orientalis* and comparable to that of *A. obstetricans*.

Dorsal buccal.—*B. orientalis* shares with *A. obstetricans* the V-shaped posterior margin of the pharynx. In *B. orien-*

talis the pharynx is longer and narrower such that the roof of the mouth is more diamond-shaped rather than typically triangular in ventral profile. The prenarial arena is like that of *A. obstetricans*, except that *B. orientalis* lacks the dorsal reflection of the beaks. The internal nares are so similar in *A. obstetricans* and *B. orientalis*, that only differences are presented here. In place of the anteriorly directed flaps of the anterior walls are a cluster of minuscule attenuate papillae on each side in *B. orientalis*. The huge flaps of the anterior narial walls are larger in *B. orientalis* than in *A. obstetricans*, but are more uniform in width. They extend postero-medially over a greater portion of the postnarial arena. Two small, conical papillae with fine apical irregularities are present in the small postnarial arena in a transverse line just anterior to the median ridge. The median ridge is identical to that of *A. obstetricans*, except that fine secondary cusps are clustered on its ventral corner rather than along the lateral margins. Lateral ridge papillae and BRA papillae are absent. Randomly dispersed about the buccal roof between the median ridge and the glandular zone are a half dozen tiny, pointed papillae and an equal number of faint pustulations in this specimen. The glandular zone is of similar proportions to that of *A. obstetricans* but the anterior margin is V-shaped, paralleling the back of the pharynx. Well-defined secretory pits are visible only at the anterior margin of the zone. The dorsal velum is slightly longer than that of *A. obstetricans*, but still shorter than that of pond hylids, at least laterally. The velum is broadly interrupted medially and has smooth medial margins reflected posteriorly.

Dorsal pharynx.—The pressure cushions are normal in terms of general size and depth, though the medial pressure cushions are slightly narrower. The ciliary groove is similar to, but even broader than that of *A. obstetricans*.

Diagnostic summary.—The following set of oral characters readily distinguishes *Bombina orientalis* larvae from all other discoglossid tadpoles studied: single, medial bifurcated, lingual papillae; buccal roof arena absent; secretory pits present only at the anterior margin of glandular zone.

Discoglossus pictus Otth
(Fig. 8)

Material.—Author's collection (stage 33; sv. 7.7 mm). Laboratory raised specimens, initially collected near Lyon, France; no date.

Reference.—Boulenger, 1891.

External.—*Discoglossus pictus* larvae have a single, medial spiracle and a relatively ventral mouth with two upper and three lower denticle rows. Typically all denticle rows are double but the outer rows may be single.

Ventral buccal.—*D. pictus* is described by comparison with *Alytes* and *Bombina*. The floor of the oral cavity is more pointed in *D. pictus* than in *A. obstetricans* and in general proportions more closely resembles *Bombina* than *Alytes*. Infralabial papillae are similar to those of *Alytes* only smaller. A few pustulations occur around the base of these papillae. The tongue anlage has six papillae with robust bases and pointed apices arranged in an arc with the most medial papillae most anterior. The medial two papillae are fused at their base and resemble the single lingual papilla seen in *Bombina*. A half dozen tiny pustulations occur anterior to the lingual papillae on the tongue anlage. The BFA is surrounded by 8 major papillae on each side, aligned in straight rows beginning at the medial margin of the buccal pocket and converging posteriorly, and an equal number of minor papillae near their bases. The BFA papillae are simple, attenuate cones lacking any major secondary pustulations or papillae. The arena is particularly well demarcated anteriorly because of large pustulations that run on each

side in a row from the lateral edge of the tongue anlage to the medial edge of the buccal pockets. There are no pustulations within the BFA and only a few very tiny pustulations on the buccal floor anterior to the pockets. Prepocket papillae are absent. Buccal pockets are shallow and unperforated, as in *Bombina*. The free velar surface has a thick glandular edge with a cusp projection over each filter cavity. The median notch is very weak.

Ventral pharynx.—The branchial baskets have similar shape and proportions to those of *Alytes*. Counts for numbers of filter rows run 9, 10, 9, and 5 for cb. 1-4. In all details of the filter rows and filter plates *D. pictus* is virtually indistinguishable from *Alytes* and *Bombina*. The branchial food traps are covered with small but distinct secretory pits, which do not appear to be organized as rows or ridges anywhere in the pharynx. The glottis is not strongly elevated; its lips are thick, but not as thick as those of *Bombina*. Approximately one-third of the glottis lies under the ventral velum. In overall proportions the glottis of *D. pictus* is most similar to that of *Alytes cisternasii* among its near relatives. *D. pictus* shares a large esophageal funnel with other discoglossoid tadpoles.

Dorsal buccal.—In shape and proportions the roof of the buccal cavity is similar to that of *Bombina*. The rostrum is not strongly turned ventrally and the prenarial arena is devoid of any surface irregularities, pustulations or papillae. The large flaps that arise from the anterior wall of the nares in other discoglossoids are present in *D. pictus*. They have a jagged, irregular free margin and are not as large as in *Alytes* or *Bombina*. The median ridge is similar to that of *Bombina*. There are a few pustulations in the postnarial arena but papillae in that region, as well as lateral to the median ridge, are absent. Ten simple papillae arranged roughly in an arc (with the crown most posterior) define the posterior edge of the BRA. A few tiny

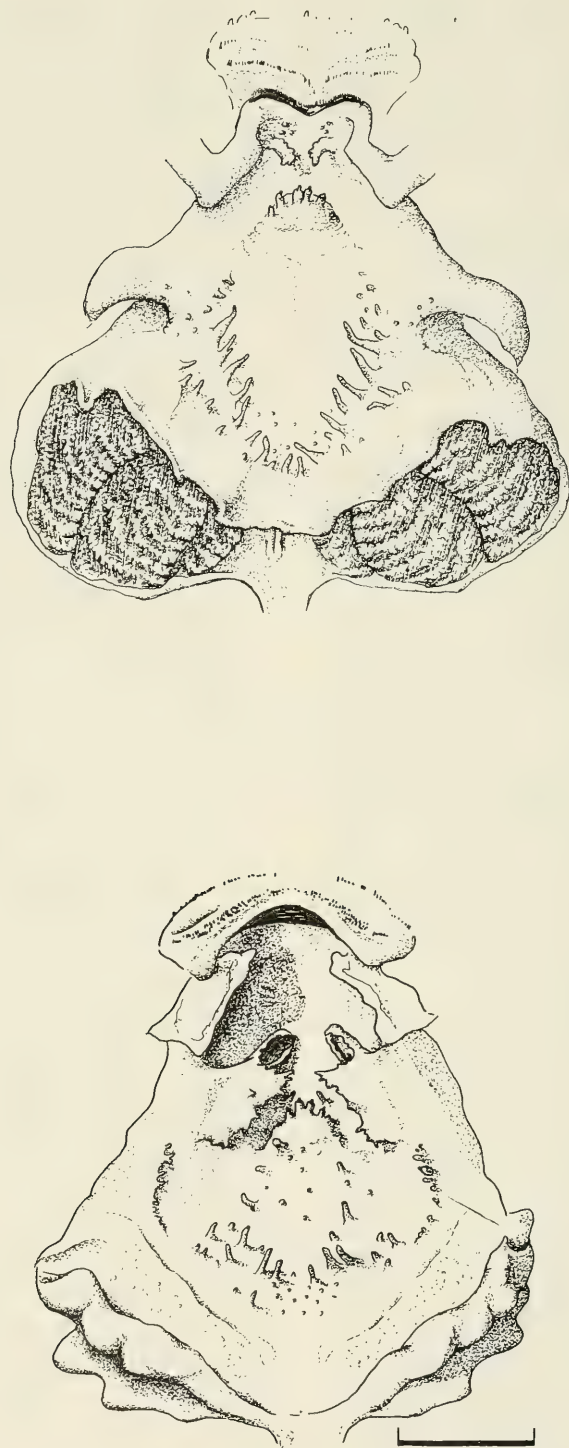


FIG. 8.—Drawings depicting *D. pictus*; floor of mouth (above) and roof (below).

papillae on one side define the lateral margin of the BRA. Several dozen small pustulations occur within the BRA among the papillae that define it. Lateral to the BRA the buccal roof is smooth with the exception of a small longitudinally oriented pustulate ridge in the far lateral margin of the buccal roof on each side. The glandular zone has a V-shaped anterior margin and is of uniform length. Small tightly packed secretory pits are visible everywhere on the glandular zone. The dorsal velum is short, weakly curved and broadly interrupted on the midline.

Dorsal pharynx.—The dorsal pharynx is indistinguishable from that of *A. obstetricans*.

Diagnostic summary.—The great similarity of all the discoglossid tadpoles masks their minor differences. Only trivial features distinguish *D. pictus* from the *Bombina* and *Alytes* larvae examined; e.g., papillation is generally greater than in *Bombina*, the arch of papillae on the tongue enlarge is different than either *Alytes* examined, the sculpturing of the ventral velar margin is least in this genus, etc. Many of these differences may be size related.

RHINOPHRYNIDAE

Rhinophrynus dorsalis Dumeril & Bibron
(Fig. 9)

Material.—Uncatalogued, author's collection (stage 36, sv. 15.5 mm). Collected in shallow pools of flooded drainage ditch along Highway 190 approximately 1.0 km north of Tehautepec, Oaxaca Province, Mexico; July 17, 1970.

References.—Orton, 1943; Stuart, 1961; Starrett, 1973; Wassersug, 1972.

External.—*Rhinophrynus* larvae have a wide oral orifice that lacks an oral disc. Keratinized structures, both denticles and beaks, are absent. There is a single, short barbel that extends forward from the middle of the lower lip in the larvae from this population. Spiracular openings are paired and bilaterally symmetrical in the genus.

Ventral buccal.—The wide oral opening of this larva gives the front of the mouth a gently curved outline in dorsal view. On the lower lip, near the midline, are two pairs of tiny, thin papillae and some extremely small pustulations. Because the lower lip curls backward inside the mouth, the more ventral pair of papillae are obscured from view without stretching the lips. Lingual papillae are absent. BFA papillae are clustered along a broad arc, all well behind the buccal pockets; they do not circumscribe an "arena" *per se*. These papillae, seven per side, are simple, anteriorly curved structures, large and of subequal size. The largest papillae are nearest the midline and displaced anterad. None of the papillae are bifurcated, although two on each side show some basal fusion. Within the arc of the BFA are two, small, attenuate papillae behind the buccal pockets near the midline. Prepocket papillae are absent. There are no papillae anywhere anterior to the buccal pockets, but above the massive ceratohyals are numerous, randomly scattered pustulations and subpapillate projections. The buccal pockets are very wide, deep and not long. They do not appear perforated. There is a large single fold of epithelium arising from the floor of the pockets. The free velar surface is not large. It is unusual in that it is fused medially with the dorsal margins of the fourth filter plates rather than continuous across the midline. The velar margin is also fused to the top of the filter plates on cb. 2 but is free for a short distance along cb. 3. Spicular support for the velar margin is absent and the velar surface tends to arch upward above each filter cavity. Except for the points of attachment, the velar margin forms a rather smooth arch when viewed from above. Posterior projections of the velum above the filter cavities and in the median notch are absent. Secretory pits could not be resolved anywhere along the posterior velar margin. The division of the velum into two parts

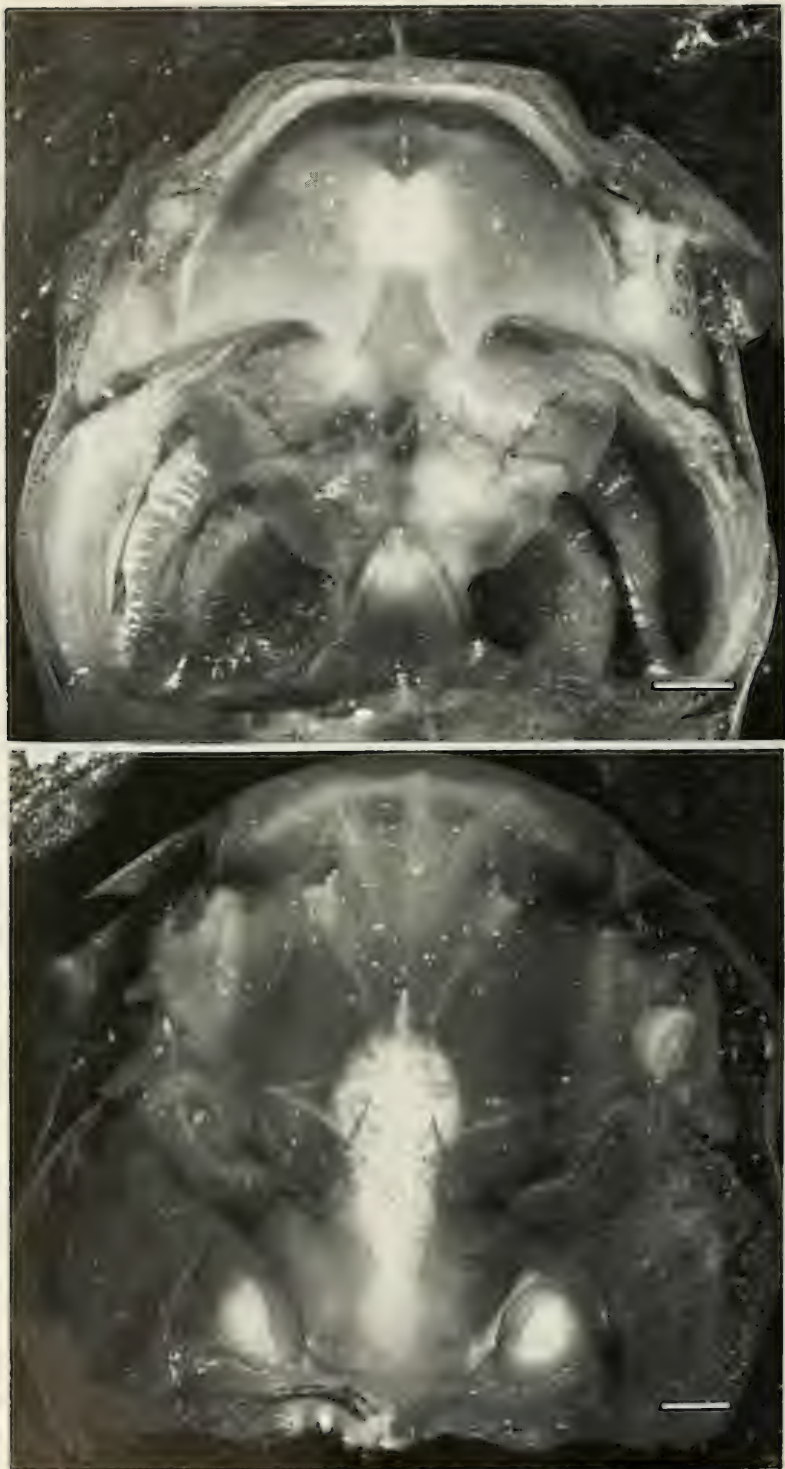


FIG. 9.—Photographs of the floor (above) and roof (below) of the mouth of a *Rhinophrynus dorsalis* larva.

means that the glottis is fully exposed above the velum and is within the buccal cavity. The glottis has a predominantly horizontal orientation, but is tipped slightly forward. A slight depression makes the anterior margin of the glottis stand out from the buccal floor. The glottal lips and laryngeal disc are comparable in size and shape to those of typical pond tadpoles.

Ventral pharynx.—The branchial baskets have a "typical" length to width ratio, but encompass an atypically large proportion of the total oral volume. The first and second filter cavities are strongly bowed outward; the third filter cavity is round and very open when viewed from above. The extreme curvature of the filter plates make it difficult to estimate height to length ratios. The relatively tall filter plates are also thick. These plates are arched through the transverse plane in such a manner that they are more imbricated away from the midline than toward the midline. Counts for filter rows run 11, 13, 13, 8 for cb. 1-4. The filter ruffles are very dense. Secondary and tertiary filter folds are very long and higher order folds are numerous. Full filter rows are very wide, particularly ventrally. The filter cavities are tall, nearly completely canopied passages. They were packed with fine silt in this specimen and other individuals from this population. With careful manipulation it is possible to curl forward the velar margin and expose some of the secretory ridges of the branchial food traps. The food traps are quite tall and narrow, but their full area cannot be determined without sectioning. The secretory ridges are not continuous from one filter cavity to the next. The ridges are tall, thin, and highly regular. The esophageal funnel is of normal proportions.

Buccal roof.—The roof of the oral cavity is far more squarish and less triangular in *R. dorsalis* than in any beaked tadpole. The buccal roof is basically flat, but has some depressions and ridges not

observed in any other species. Smooth transversely oriented ridges occur on each side of the roof formed by an abrupt rise just posterior to the articulating surface of the ceratohyal with the palatoquadrate bars. These ridges, which do not cross the midline, align with buccal pockets below. More posteriorly within the glandular zone are three concavities of the roof on each side. These correspond to the upwellings of the free velar surface over each filter cavity. The middle concavity on each side is the largest and has a steep, transverse anterior wall. The lateral and medial pairs are more gentle, shallow hollows. The internal nares are tiny and far anterolateral; a prenarial arena is ill-defined. Anterior to the nares are a half dozen small, scattered pustulations. The narial openings are small transverse ovals, slightly larger medially than laterally. Their anterior and medial margins are weakly defined and have a faint texture. Prenarial papillae are absent. The posterior narial walls are thin flaps, more horizontal than vertical, and about as wide as tall (*vide long*). Narial valve projections are absent. The median ridge and papillae of the buccal roof that demarcate postnarial and buccal roof arenas in other tadpoles are absent. Several dozen pustulations are dispersed over the buccal roof between the nares and the glandular zone. There are also two pairs of small, blunt papillae in the midportion of the buccal roof halfway between the midline and lateral margin; they are the only symmetrical projections of the buccal roof. The glandular zone is made up of dense, moderately large and conspicuous secretory pits that extend back onto the pressure cushions. Although the anterior margin of the zone is quite wavy, the zone is of generally uniform length except directly in front of the esophagus where it abruptly decreases to a negligible length. The average length of the zone is equal to or slightly greater than in typical pond larvae. The dorsal velum is shorter and

not particularly coiled. It is rather stiff, projects directly anterad, and is absent on the midline.

Dorsal pharynx.—As viewed from above, the dorsal pharynx on each side is shaped like a right, isosceles triangle with sides posterior and lateral, and the hypotenuse facing anteromedial. The pharynx is larger than in any beaked tadpole, with pressure cushions extending back well past the posterior margin of the dorsal velum. There are three pairs of very large, distinct pressure cushions. The most lateral pairs are tall, oblique ridges with sharp ventral edges. The middle pair are oriented like the lateral pair, but are not as tall and have a posterior knob rather than a continuous sharp edge. The medial pair are large, round swellings. Behind the pressure cushions is a relatively narrow and shallow ciliary groove.

Diagnostic summary.—The full attachment of the ventral velum to the tops of all filter plates, including those of cb. 4, immediately separates *Rhinophrynus* from all other species. The following is a partial list of other features which, in combination, diagnose *Rhinophrynus*: lingual papillae absent; massive prepocket buccal surface; buccal floor arena papillae in broad arch; glottis exposed on posterior buccal floor; absence of velar marginal projections; massive branchial baskets; well-developed secretory ridges; absence of all features that would outline postnarial and buccal roof arenas; presence of lateral depressions of buccal roof above buccal pockets.

MICROHYLIDAE

Microhyla berdmorei (Blyth)

(Fig. 10)

Material.—FMNH 187567 (stage 32, sv. 10.8 mm). Rock pool adjacent to flowing stream at Khao Yai, Nakhon Ratchasima, Thailand; January 5, 1969.

References.—Inger, 1966 (p. 150); Heyer, 1973.

External.—*Microhyla berdmorei* tadpoles are of medium size for the genus. As is characteristic of the family, they lack hard mouth parts and have a medial spiracle. In *M. berdmorei* the tail is pointed but lacks a vibrating filamentous tip.

Ventral buccal.—The floor of the mouth is shaped somewhat like a trapezoid (base posterior) with the length and width approximately equal. The buccal floor behind the buccal pockets is extremely elongate. The ceratohyals are so short, compared to the length of the branchial baskets, that only a fifth of the mouth is anterior to the buccal pockets. The tiny lower lip is directed dorsally. There are three small, blunt infralabial papillae on each side concentrated within the loop of the lower lip. The most anterodorsal papilla is a small, simple knob-like projection. There is an anteroventral papilla slightly more attenuate. The third papilla is posterior. It is a thick, transversely oriented flap that has a common ventral base with the anteroventral papilla. The posterior infralabial papillae from each side abut at the midline, obscuring much of the oral orifice. The tongue anlage is an elongate oval devoid of lingual papillae. The BFA papillae are arranged along a semicircle which is open anteriorly. The front edge of the arena is formed by the buccal pockets. The arena is substantially wider than the relatively short interpocket distance, but limited to the anterior half of the portion of the buccal floor behind the pockets. The papillae are small, attenuate cones, evenly spaced and lacking terminal irregularities. I counted five on one side and six on the other, with the largest ones most posterior. Arising from the center of the buccal floor at the back of the arena is the glottis—a remarkable anterad displacement from the typical mid-pharyngeal position of this structure in all tadpoles with beaks. The elevated laryngeal disc is tipped so the glottis is directed anterodorsally. The glottal slit

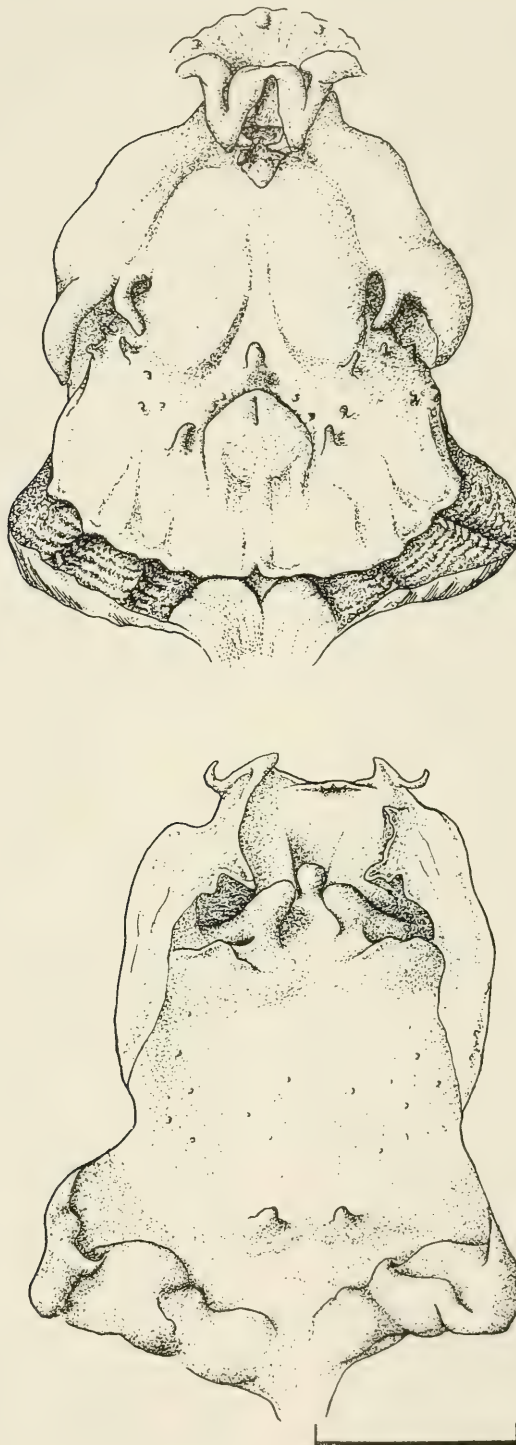


FIG. 10.—Drawings of the floor (above) and roof (below) of the mouth of a *Microhyla berdmorei* larva.

is of moderate size with very weak lips. Directly in front of the glottis is a single, small medial papilla. A single, conical, mediodorsally directed prepocket papilla can be found on each side. There are a few faint pustulations within the arena that disperse out over the lateral arms of the ceratohyals. A long trachea is visible in the buccal floor, dividing the BFA and the rest of the buccal floor, including the edge of the velum, into right and left halves. The buccal pockets are very large triangular pouches with their posterior margins far more obliquely oriented than in any hyliid examined. The pockets are not deep compared to their unusual length, nor are they perforated. The velar surface is astonishingly long—about half the length of the mouth. The freely movable portion of the velum is, however, only slightly longer than in typical pond larvae. Spicular support is absent from this delicate surface. The velar margin lacks any posterior projections and forms a smooth arc as viewed from above. The margin is reflected dorsally along its medial edge where it joins the trachea. Secretory pits scattered along the posterior velar edge are limited to the absolute margin; these pits are few in number and quite small in size.

Ventral pharynx.—The volume of the branchial baskets is over half of the total volume of the head and body; i.e. larger than in any beaked tadpole. The increase is primarily in length, with the baskets extending so far forward that almost half of the baskets are under the velum. Viewed from above, the baskets are basically shaped like elongate triangles and have their long axes oriented closer to the sagittal plane than in any beaked tadpole examined. The filter cavities decrease in size as one goes from the first to the third. The filter plates are almost vertical, except that a slight arch to the top portion of the third plate blankets the top of the third filter cavity. The extension of the filter plates under the velum makes the more anterior filter

rows inaccessible without dissection of the ventral velum. Counts for filter rows run 22, 20, 18, 10 for cb. 1-4, exceeding the values for any beaked tadpole. The filter rows have normal proportions in terms of folding pattern, but are not quite as tall as in typical pond larvae. Neighboring filter rows fully abut and tertiary folds from neighboring rows interdigitate. The filter canals are very small, fully canopied tubes. The branchial food traps are unlike any seen in beaked species. They are slender, vertical crescents of a thick secretory tissue (hence the name crescentic organs; Savage, 1952), isolated at the anterior end of the filter cavities and inaccessible without dissection of the velar surface. The area covered by the organs is very small compared to the size of the filter cavities. Secretory ridges are very dense within the food traps and are not easily resolved in this specimen. Bound by the narrow crescentic organs are vertical regions of the filter cavities containing a few, loosely defined clusters of secretory cells. Most of the ventral surface of the velum is free of secretory tissue of any sort. The esophageal funnel is both narrow in profile and small in diameter.

Dorsal buccal.—The roof of the mouth shares with the floor a trapezoidal, almost rectangular profile. In details, the roof differs radically from all non-microhylids examined. The upper lip is nearly horizontal so that the pre-narial arena is large and square. Far back in the arena, in line with the front of the internal nares is a single, medial, conical papilla, which is anteriorly curved and of medium size. Other surface features are absent. The most unusual aspect of the roof is the internal nares. Each naris is a shallow, round cul-de-sac with all but the lateral third covered by a textured, presumably sensory, tissue patch. Thin, flap-like vertical walls surround the medial edges of these narial depressions. The antero-medial portions of the walls are low and coarsely serrate; the posteromedial por-

tions are relatively huge, tongue-like flaps that project anteriorly under the nares and touch on the midline. These projections are in a position corresponding to that of the narial valve projections in some beaked tadpoles. While they may be homologues to the narial valve projections, they are clearly not associated with any functional valves, for the nares are not perforated. These projections are strongly concave anterad. A vertical ridge descends down the posterolateral surface of each projection and clearly stiffens it. The bases of these ridges align with a small triangular flap on each side of the buccal pocket just posterolateral to the nares. The nares lack any sort of rim or wall along their whole lateral margins. A postnarial arena is absent. There are no postnarial papillae, lateral ridge papillae, or median ridge to define this arena. Halfway back on the buccal roof are four simple, conical BRA papillae. These papillae are too close to each other and to the midline to define a buccal roof arena. On each side of the midline, the smaller of the two papillae is displaced slightly anterolaterad. Beginning lateral to the BRA papillae and extending in a straight row anterolaterally across the buccal roof is a series of evenly spaced pustulations on each side. There are a few, very thin pustulations scattered over the buccal roof anterior to the BRA papillae; otherwise, papillae and pustulations of the buccal roof are absent. The glandular zone is of typical length. Its anterior margin is nearly transverse. The secretory pits are large and conspicuous, but of very low density. The dorsal velum at its maximum length is 25% longer than that of common pond hyliid larvae. It is continuous across the midline, although rather abruptly constricted in that region.

Dorsal pharynx.—The two pressure cushions on each side are quite distinctive. The lateral one is, on the average, twice as long and tall, and four times as wide, as the medial cushion. Its tall-

est point is at its posterolateral corner, where it is nearly twice as tall as at its midpoint. The medial cushion is more precisely defined and of more uniform proportions. Laterally, the ciliary groove of *M. berdmorei* is shallow and very wide. Medially, the groove becomes a narrow, deeply entrenched canal.

Diagnostic summary.—Microhylid larvae differ from all other tadpoles in the attachment pattern for their ventral velum to their filter plates, the position of the glottis, the shape of the branchial food traps, and structure of the unperforated internal nares.

Microhyla berdmorei is readily distinguishable from the other microhylids examined by the combination of: large, medially abutting, posterior infralabial papillae; a single preglottal papillae; high count of filter rows; narrow branchial food traps; four buccal roof papillae; dorsal velum vestigial medially.

Microhyla heymonsi Vög
(Fig. 11)

Material.—FMNH 187923 (stage 37, sv. 6.8 mm). Small pool above dammed stream at Sakearat Experimental Station, Amphoe Pak Thong Chai, Changwat Nakhon Ratchasima, Thailand; February 24, 1969.

References.—Parker, 1934 (p. 135); Heyer, 1973.

External.—Besides the beakless mouth and median spiracle typical of microhylid larvae, the tadpoles of *Microhyla heymonsi* are characterized by an oral disc expanded into a large, upwardly directed funnel. Only features which distinguish these larvae from the two previously described species of *Microhyla* are dealt with in the following description.

Buccal ventral.—Anteriorly the floor of the mouth is broad and gently curved, when viewed from above. Posteriorly, the branchial baskets are truncated. The prepocket portion of the buccal floor is much elongated compared to other spe-

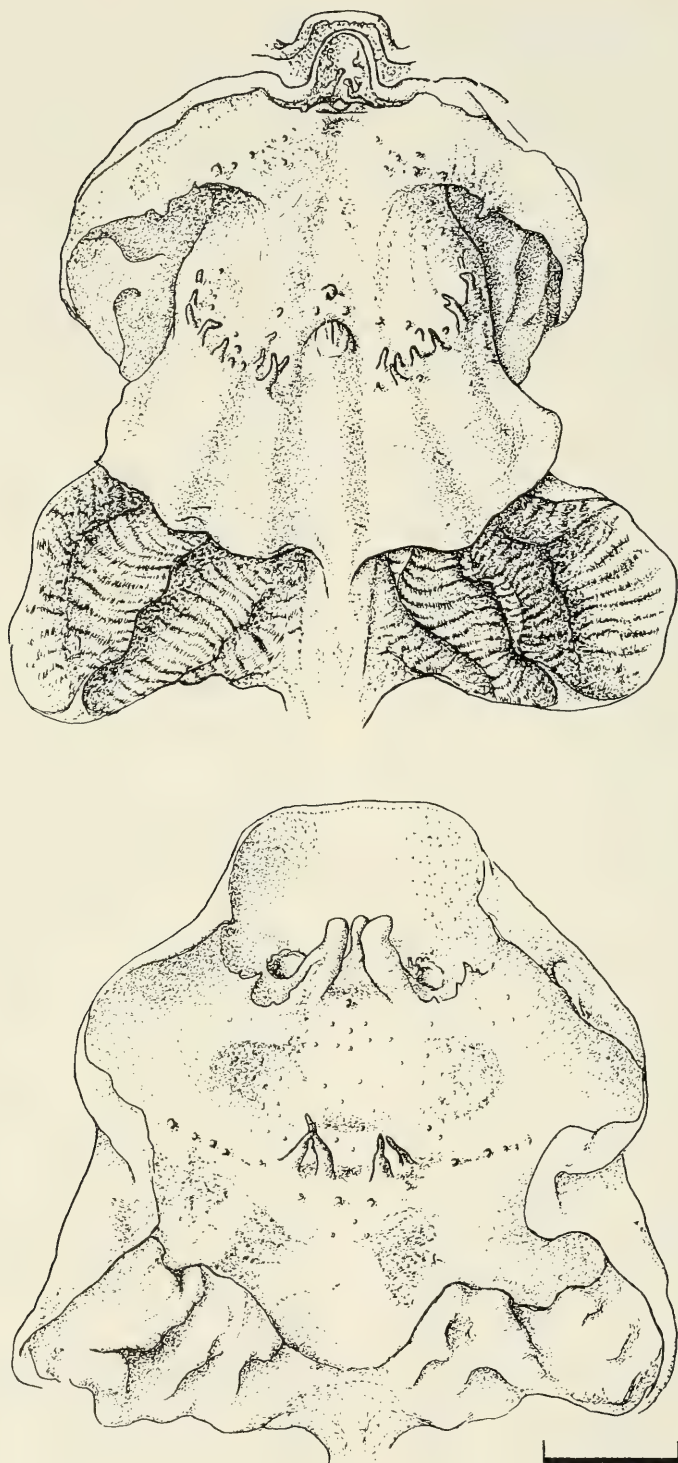


FIG. 11.—Drawings of the floor (above) and roof (below) of the mouth of a *Microhyla heymonsi* larva.

cies of *Microhyla*. The posterior shift of the buccal pockets reflects the unusual shape of the underlying ceratohyals. These are extremely elongate medially and have posteriorly directed lateral arms. The infralabial papillae are as in *M. berdmorei*. BFA papillae are reduced in size and number (3 on one side and 4 on the other), grading into pustulations. The papillae are blunt rather than conical. There is a single, blunt, medial papilla in front of the glottis. Prepocket papillae are large and strongly curved medially. The buccal pockets are narrow, nearly longitudinally oriented slits. They are deep and their floors inaccessible without further dissection; whether or not they are perforate was not determined. The glottis, which lacks elevated lips, sits on a huge laryngeal disc. It is directed dorsally and positioned about two-thirds of the distance back on the buccal floor. The trachea is much shorter in this species than in the other *Microhyla*. The velar margin is gently arched and lacks any projections. It is virtually continuous over the trachea, but left and right sides are interrupted by a small median notch. Secretory pits could not be resolved on the velar margin.

Ventral pharynx.—The branchial baskets are shaped like equilateral triangles with more than half of the filters under the velar margin. The baskets are tiny, being proportionally smaller even than those of typical, Orton type 4 pond larvae. The third filter cavity is reduced in size and nearly inaccessible under the velum. All filter cavities contained fine, flocculent food matter in this specimen. Counts for filter rows on each filter plate were well below those for other *Microhyla* (and within a row of the counts for *H. regilla*). The filter mesh is not as dense as in the other *Microhyla*. Fine tertiary and higher order filter folds are lacking. Well-developed secretory ridges are present anteriorly under the ventral velum. Although the branchial food traps seem relatively larger than in

the other two species, the full extent of the traps could not be determined because of difficulty in staining and the small size of these tadpoles. The ridges were absent along most of the unattached velar surface. The esophageal funnel was slightly larger and broader than in the two other species.

Dorsal buccal.—There is a small, posteriorly directed V-shaped depression in the middle of the prenarial arena. A single, medial papilla of the prenarial arena arises at the posterior apex of this V-shaped concavity. This papilla is small, straight, and blunt. The extent of the presumed sensory patch in the internal nares could not be determined. The narial walls are more similar to those of *M. ornata* than to *M. berdmorei*. The anteromedial portions of the narial walls are reflected backward under the narial openings. The bases of the large, posteromedial projections of the narial walls are widest in this species. The ridges on the backs of these projections are not as tall in *M. heymonsi* as in *M. ornata* or *M. berdmorei*. They are, however, more sharply defined and completely continuous with the small flaps posterolateral to the nares. In *M. heymonsi* these flaps have arched rather than pointed apices. There are two tiny, blunt papillae far posterior on the buccal floor and several dozen blunt pustulations dispersed over the surface in a W-shaped pattern. I could resolve secretory pits, but only on the dorsal velum. The glandular zone, as a discreet region of the buccal roof, may be absent. The dorsal velum is shorter than in the other two species, at least in the neighborhood of the midline; nevertheless, the velum is still continuous across the midline.

Dorsal pharynx.—Only lateral pressure cushions are well-defined and these are small, obliquely oriented ovals, much smaller than the medial pressure cushions in the other species. The ciliary groove is comparable to or slightly deeper than that of *M. ornata*.

Diagnostic summary.—The mouth of

M. heymonsi grossly differs from the mouth of the other *Microhyla* in the following features: longer prepocket buccal surface; ventral velum virtually continuous across the midline; branchial baskets highly reduced; very large esophageal funnel; V-shaped groove in prenarial arena; dorsal velum and pressure cushions reduced.

Microhyla ornata Dumeril & Bibron

Material.—Uncatalogued, author's collection (stage 36, sv. 5.9 mm). Collected in shallow cement drainage ditch on the grounds of Applied Scientific Research Corporation, 196 Eahoyothin Rd., Bangkok, Bangkok, Thailand; August 22, 1968.

Reference.—Lui, 1950 (p. 251-252).

Microhyla ornata is so similar to *M. berdmorei* that only the differences are presented here.

External.—*Microhyla ornata* is a small species with small tadpoles. Its larvae can be distinguished externally from those of previous species by their smaller size, rounder snouts and relatively longer, filamentous tails.

Ventral buccal.—The floor of the mouth is anteriorly rounder in *M. ornata* than in *M. berdmorei*. *M. ornata* lacks anterodorsal infralabial papillae and the posterior infralabial papillae are no more than gentle swellings incapable of abutting on the midline. The medial preglottal papilla is relatively taller in *M. ornata*, and in this species there is a second smaller, medial preglottal papilla in front of the first one. The prepocket papillae are relatively larger and curved medially. The margin of the velum has a single, broad posterior projection on each side above the filter plates of cb. 3. Numerous tiny secretory pits are present in a narrow row along the velar margin medial to the apices of the posterior projections. The medial edge of the velum is not reflected posteriorly at the margins of the trachea.

Ventral pharynx.—Counts for filter rows run 14-15, 16, 13-14, 9 for cb. 1-4.

Tertiary folds on the filter rows do not interdigitate as tightly as in *M. berdmorei*, but the difference is slight enough to be accountable to minor differences in preservation. The branchial food traps are wider and form nearly complete tori. The area bound by the food traps has faintly developed secretory ridges and, unlike *M. berdmorei*, these extend posteriorly onto the ventral surface of the ventral velum but are still absent along the posterior velar margin.

Dorsal buccal.—Walls of the internal nares are not as tall as in *M. berdmorei*. The anteromedial portions lack serrations; the shorter, posteromedial projections do not meet each other on the midline. The ridges on the back of these projections are very faint. The presumed, sensory field in the internal nares covers a greater portion of the narial depressions. *M. ornata* has two rather than four BRA papillae. They are relatively taller than the BRA papillae of *M. berdmorei*. The rows of pustulations extending away from the BRA papillae are less conspicuous. The secretory pits of the glandular zone are even less dense than in *M. berdmorei*. The zone is fragmented into four approximately equal portions with one division along the midline and two other divisions between the midline and the lateral buccal margin. The glandular zone ends anterior to the base of the velum. The dorsal velum is more complete across the midline. Rather than being just a vestige, the mid-portion of this flap is equal to a fifth of the maximum length of the velum.

Dorsal pharynx.—Differences are minor and attributable to preservation.

Diagnostic summary.—*Microhyla ornata* is virtually identical to *M. berdmorei*. The few differences—*viz.*, infralabial papillae not abutting, double preglottal papillae, less filter rows, 2 buccal roof papillae, dorsal velum more complete across midline—may largely be ascribable to the differences in size.



FIG. 12.—Photographs of the floor (above) and roof (below) of the mouth of a *Scaphiopus bombifrons* larva.

PELOBATIDAE

Scaphiopus bombifrons Cope

(Fig. 12)

Material.—FMNH 75020 (stage 36, sv. 15.5 mm). Collected from drainage ditch 4.6 km west of Fredrick, Tillman Co., Oklahoma; July 4, 1948.

References.—Stebbins, 1951 (p. 205-207); Bragg, 1965 (p. 63-91).

External.—The head is broad; the spiracle is sinistral. The oral disc is moderately small but surrounds a large and powerful beak. The most common denticle pattern is 4/4 but both the upper and lower rows may range from 2 to 6 in number (Bresler and Bragg, 1954).

Ventral buccal.—The floor of the mouth in dorsal view closely approximates an equilateral triangle. There are two pairs of moderate sized infralabial papillae. The first pair is far anterior within the arc of the infralabial cartilage; these project anteriorly out of the mouth. The second pair is positioned more dorsolateral and posterior, and projects medially. All four papillae are subequal in size, slim, slightly compressed cylinders and lack marginal papillae. The lingual papillae are typical in height and orientation, although they may have a slightly enlarged basal diameter. The apices of the papillae are covered with fine pustulations. The buccal floor arena is a poorly defined, egg-shaped patch bearing between 40 and 50 papillae. Those papillae around the edge and within the patch are rather homogenous; they are all evenly spaced, medium small, straight and a few have fine terminal pustulations. Posteriorly, the papillae are replaced by pustulations. Papillae and pustulations are absent directly in front of or behind the buccal pockets, which are very narrow, transverse depressions. The pockets are shallow and unperforated. The free velar surface has an average relative area but otherwise is quite unusual. The margin of the velum is a wide, smooth edged "V," with each side being nearly

straight or slightly convex anteriorly. There is a short, but relatively wide, median notch. The velum is supported by only two pairs of spicules. One pair neighbors the midline and the other is nearby, directly over the filter plate of cb. 4. The spicules are wide and not very stiff. Small but dense and conspicuous secretory pits form a band along the posterior velar margin. The band is widest around the median notch and thins out laterally so that secretory pits are absent along the lateral quarter of the velar margin.

Ventral pharynx.—The branchial baskets are close to perfect ovals with the long axes of the ovals running antero-laterad to posteromesad. The baskets are moderately shallow. They are of average or slightly larger than average size. The filter plates of the second and third ceratobranchials do not project upward, consequently, each basket is a single common filter cavity. Counts for filter rows run 10, 14, 10-11, 9 for cb. 1-4. These are all above the average; those for cb. 2 and 4 significantly so. The filter mesh on each filter row is very fine due to multitudinous tiny, tertiary filter folds on each secondary fold. The filter mesh, however, is not dense—rather wide gaps exist between neighboring filter rows. (The distance between rows may have been slightly accentuated by shrinkage from preservatives.) Some of the rows, particularly those of cb. 2 and 3, are wider than normal. The filter canals are very tall and moderately wide. They are about 80% canopied by the filters. The ventral surface of the velum is covered by buff textured tissue, indicative of a secretory mucosa. At 75 \times magnification no organized ridges or secretory pits could be resolved. This species presumably lacks secretory ridges. The glottis, glottal lips and laryngeal disc are typical in size and shape. The glottis is fully visible on the pharynx when viewed from directly above. The esophagus is large and the funnel is broad in dorsal profile.

Dorsal buccal.—*S. bombifrons* has a slightly larger prenarial arena and smaller postnarial arena than seen in a typical type 4 larva such as *Hyla regilla*. The smaller postnarial arena is the result of relative displacement on the median ridge anteriorly. The most unique feature of *S. bombifrons* is a small, round, keratinized knob in the center of the prenarial arena. Other than this, the prenarial arena is devoid of any papillae, pustulations or ridges. The internal nares are narrow, oblique slits. The anterior narial walls have slightly pustulate anteromedial corners but lack prenarial papillae. The narial valves have slightly arched margins, but lack narial valve projections. A deep groove behind each narial valve sets the valves off from the postnarial arena. The postnarial arena is bound laterally by two medium sized, robust papillae aligned directly behind the medial edges of the nares. These two papillae have pustulate crowns and a secondary, short, conical papilla at their lateral bases. A single, tiny, pointed papilla occurs posterolateral to the two postnarial papillae. The median ridge is a moderately tall, triangular flap with a relatively shorter base. The ridge is thick and stiff. There is a single, large, pointed, asymmetric, marginal projection on the median ridge in this specimen. The anterior surface has pustulations, but they are concentrated in a rim around the edge of the flap. There are two small, pointed pustulations within the prenarial arena. A buccal roof arena is absent. Scattered about the buccal roof behind the median ridge are a few dozen pointed pustulations. Two or three of the more anterior ones are slightly larger than the others. The glandular zone is overall very wide, only narrowing slightly near the midline; its anterior margin is a distinct, broad "V." The secretory pits are uniformly large and conspicuous, but not particularly dense. The dorsal velum is very long and broadly interrupted on the midline. Each side is anterodorsally coiled.

Dorsal pharynx.—A single, massive pressure cushion covers the dorsal pharynx on each side. These cushions are deep, elongate ovals with their major axes running anterolateral to posterodorsal. The ciliary groove was damaged in dissection, but appears very broad medially.

Diagnostic Summary. — *Scaphiopus bombifrons* larvae are unique among the species examined in the following features: pattern and shape of infralabial papillae; shape of lingual papillae; shape of ventral velar margin; presence of keratinized knob in prenarial arena; size and shape of pressure cushions.

Megophrys minor Stejneger
(Fig. 13)

Material.—FMNH 49857 (stage 34, sv. 16.5 mm). Collected from pools under cascades of small mountain streams or in side pools of large mountain streams where current is slow, at approximately 9100 m elevation, near Taosze, Mount Omei, Szechwan, China; June 15, 1946.

Reference.—Liu, 1950 (p. 188-191).

External.—*Megophrys minor* larvae have a huge, upwardly directed, denticle free oral disc. They are generally thought to lack keratinized beaks, but the fine, hair-like structures at the margin of the oral orifice (noted by Liu, 1950) are undoubtedly vestiges of oral beak serrations. The tadpoles have a long, powerful tail; the spiracle is sinistral.

Ventral buccal.—The anterodorsad direction of the lower beak results from a general, dorsal curvature of the anterior portion of the mouth. Because the prepocket portion of the oral floor is relatively large and expanded anterolaterally, when the mouth is pinned flat the oral floor is in the shape of an elongate trapezoid rather than a triangle. *M. minor* has four infralabial papillae within the loop of infralabia and visible in the oral orifice of an undissected tadpole. These papillae were illustrated

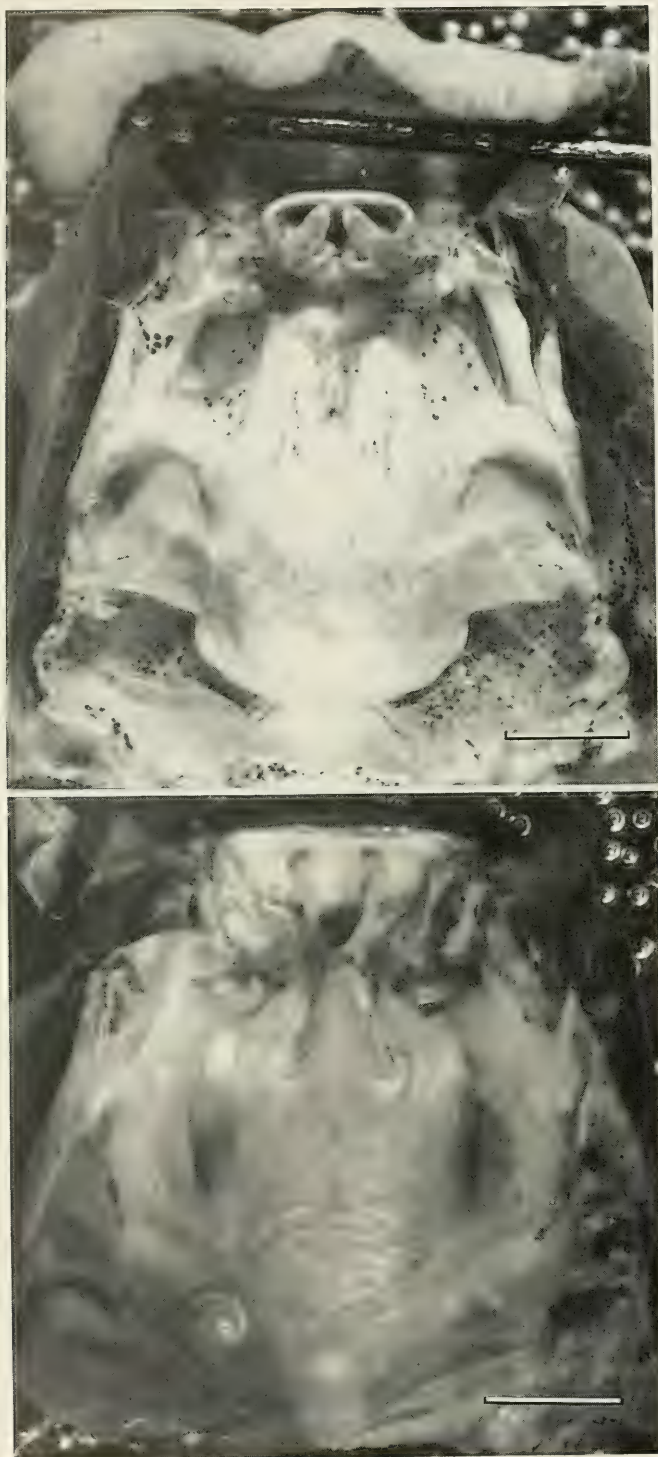


FIG. 13.—Photographs of the floor (above) and roof (below) of the mouth of a *Megophrys minor* larva.

and described in detail by Liu, 1950 (Fig. 382 and p. 190). In addition there are five other infralabial papillae, one on the midline, posterior to the visible four, and two others on each side, dorsolateral to the loop of the infralabial cartilage. All the infralabial papillae are thick, fleshy lobes that lack terminal serrations or papillae. The five most mesial papillae curve slightly anterad. The four most lateral papillae are elevated knobs. The most anterior and dorsal pair of lateral infralabial papillae are oval (anteromedial to posterolateral major axis), palp-like projections on the posterior corners of the infralabial cartilage. The more dorsal pair of lateral infralabial papillae are also oval (transverse major axis) but are smaller than the pair just described. The medial papilla is a triangularly shaped projection that fits in tightly between the smaller and more posterior pair of external visible papillae. Lingual anlage and lingual papillae were not observed in the normal position. The medial infralabial papilla could be a homologue of the lingual papillae; however, the far anterior placement of this papilla argues against such a hypothesis. Buccal floor arena papillae are absent. Instead of a BFA *M. minor* has two massive ridges that run the length of the prepocket surface of the buccal floor. Each ridge has a predominantly anterior to posterior orientation. They are slightly bowed inward and have elevated terminal knobs. The ridges are quite resilient, but not supported by cartilage. They are set off from the rest of the buccal floor by deep creases both in front and in back of them. Immediately medial to the ends of the buccal pockets are small, anteriorly concave flaps that surround the terminal knobs of each ridge. There is one blunt, rather antero-medial, prepocket papilla on each side, plus a small series of prepocket pustulations. A half-dozen stubby pustulations are scattered over the dorsomedial portion of the buccal floor. A few small pustulations are also on the buccal floor

in a narrow, transverse arch behind the buccal pockets and in an anterior-posterior line bowed outward slightly, above the lateral portions of the ceratohyals. The buccal pockets are very short and strongly arched anteriorly. Despite the fact that they are quite shallow, folds at the bottom of each pocket make it difficult to determine if the pockets are perforated. If the pockets are perforated, the openings must be extremely small. The free velar surface is moderately large and supported by long, thin spicules. The posterior margin is unusual in having a U-shaped medial margin and a straight, nearly transverse lateral margin. There is a sharp inflection point between the straight and curved portions. Posterior projections are lacking; the median notch is small. The curved portion of the posterior margin is slightly thickened and has a buffed texture; however, individual secretory pits could not be resolved, even at 75 \times magnification, anywhere along the velar margin.

Ventral pharynx.—The branchial baskets are similar in size, shape and proportion to those of other megophrynines, particularly *Leptobrachium*. As viewed from above, the baskets are oval, nearly round, and cover an area slightly less than they do in *H. regilla*. They are very shallow, and the filter plates of cb. 2 and 3 are very low so that there is only a single common filter cavity on each side. Counts for filter rows run 8, 9, 9, 7 for cb. 1-4. The first three values are insignificantly different from those of *H. regilla* while the count for cb. 4 is significantly above the *H. regilla* mean. The filter rows are quite wide, but the filter niches are larger than in other megophrynine tadpoles because the filter folds are very thin. This may be, in part, a preservational artifact. On many of the filter rows tertiary filter folds are so long that they abut with the filter folds of neighboring rows. Filter rows from opposing filter plates meet end to end above each gill slit rather than inter-

digitating, and thus they obscure the gill slits. The filter canals are small but most are fully canopied. Nevertheless, the general low density of the filter mesh makes the canals rather open, diffuse corridors. The ventral surface of the ventral velum is covered with a fine, buff textured tissue, suggesting a secretory mucosa. Organized secretory tissue, as either pits or ridges, could not be resolved at even $75\times$ magnification and is presumed absent from the branchial food traps. The glottis is small, with a typical amount of exposure posterior to the ventral velum. It has elevated lips, sits on a transversely oriented laryngeal disc, and is oriented slightly anteriorly rather than dorsally. The esophageal funnel has a moderately large bore, but a generally narrower profile than that of other megophrynine larvae.

Dorsal buccal.—The upper beak is nearly straight rather than curved, thus, the prenarial arena is very wide and the buccal roof more trapezoidal than triangular in shape. Individual papillae are absent from the buccal roof; instead rows of papillae are replaced by ridges. Projecting down from the middle third of the prenarial arena is a large, V-shaped ridge. The anterior corners of the ridge are the thickest and tallest portions and are reflected medially. There is a deep sulcus within the apex of the "V." Behind the apex a medium sized, round "knob" descends from the roof. On each side paralleling the arms of the V-shaped ridge, but far lateral, is a short, thin ridge. Posterior to the ends of these ridges and directly lateral to the apex of the V-shaped ridge are clusters of medium small, blunt pustulations. The nares are of moderate size and transversely oriented. The internarial distance is large. The anterior narial walls are slightly pustulate along their more medial halves and possess a stiff, medium tall, conical papilla along their more lateral halves. The narial valves are tall and each possesses a distinct, pointed projection. Although

the prenarial papillae and the narial valve projections are relatively tall, they are still far shorter and less attenuate than in other megophrynine larvae examined. The postnarial arena is a moderately small, smooth, triangular recess in the buccal roof. The arena is filled by the body of the median ridge, which is a massive, nipple-shaped, anteriorly directed projection. This projection extends far forward, anterior to the nares and under the posteromedial "knob" in the prenarial arena. Despite its unusual size and shape, the median ridge in *M. minor* is similar to the typical flap-like median ridge in most other species, being joined to the buccal roof along a narrow, transverse line and free to move ventrally in the sagittal plane. The postnarial arena is bound laterally by wide, low ridges that extend far posterior and are major features on the buccal roof. These ridges are the presumed homologues of the postnarial papillae and possibly the BRA papillae collectively. The ridges begin as anterad projections that extend almost as far forward as the tips of the median ridge. The ridges become the medial walls of the internal nares and bow outward along most of their length. The end of each ridge is recurved. The ridges are tallest and thinnest anteriorly, and lowest and widest posteriorly. They end just behind the middle of the buccal floor and well behind the base of the median ridge. The lateral ridge papillae are represented by large, thick, obliquely oriented flaps, far lateral to the middle of the ridges just described. On each side anterolateral to these flaps is a similar subsidiary projection. These subsidiary lateral ridge "papillae" are only a third to a half the size of the main ones. Posteromedial to the main lateral ridges are small ridges each with a gently crenulate margin and a predominantly anterior-posterior orientation. These ridges are in a position comparable to the lateral roof papillae seen in many tadpoles and are presumed homologues of these struc-

tures. They blend posteriorly into a cluster of pustulations. A buccal roof arena is absent. Pustulations are present behind the median ridge and mesial to the posterior arms of the long ridges that bound the postnarial arena. There is also a loose cluster of faint, blunt pustulations in the posteromedial portion of the buccal roof. The glandular zone is narrow and thins out toward the midline; it is absent in front of the esophagus. The secretory pits at the anterior margin of the glandular zone are elongate in an anterior-posterior direction. The remaining secretory pits are relatively heterogenous in size and shape, but the larger and rounder pits tend to be along the posterior margin of the zone. It is difficult to separate the dorsal velum from the pressure cushions for the velum seems very short and directed ventrally rather than anteriorly or anteroventrally. This may, however, be an artifact from shrinkage. The velum is broadly interrupted medially and the medial margins on each side are reflected dorsally into the esophageal funnel.

Dorsal pharynx.—*M. minor* has only one large pressure cushion per side. The cushion is tallest and widest far lateral and triangular in shape. The ciliary groove was damaged in dissection and its proportions could not be determined in this specimen.

Diagnostic summary.—*Megophrys*, as represented by *Megophrys minor*, differs from all other tadpoles examined in the structure of the infralabial papillae; shape of the ventral velar margin; large, nipple-shaped median ridge and large lateral ridge papillae.

Leptobrachium hasselti Tschudi

(Fig. 14)

Material.—FMNH 14828 (stage 35, sv. 27.8 mm). Swampy area adjacent to stream at Labang Camp on Sungei Seran, Bintulu District, Fourth Div., Sarawac, Borneo; November 5, 1963.

Reference.—Inger, 1966 (p. 33-36).

External.—*Leptobrachium hasselti* tadpoles commonly have a 6/6 or 7/6 denticle pattern but there is both zoogeographic and ontogenetic variation in the number of denticle rows (see Inger, 1966, Table 3). The spiracle is sinistral. The body is deep and the tail is shorter than in most megophryine tadpoles.

Ventral buccal.—The floor of the mouth is broad despite the fact that anteriorly the oral orifice is comparatively small. There is a single, major hand-shaped infralabial papilla on each side which is typical in size, shape and position but with marginal "fingers" long and attenuate. Between the lateral margin of the keratinized beak and the infralabial papilla is a series of three papillae or pustulations in a straight anterior to posterior row. The largest is the most anterior one. Ventral and medial to the hand-like infralabial papillae are two moderately tall, attenuate papillae. These have pustulate surfaces. Lingual papillae are not evident on the tongue anlage but the two papillae just mentioned could be possible analogues or even homologues of the lingual papillae. The buccal floor arena is well defined by 10-12 moderately large, attenuate, conical BFA papillae on each side and a field of 20 or more smaller, but similarly shaped papillae posteriorly. The lateral BFA papillae are aligned parallel to the sagittal plane. The tallest ones show some slight, marginal pustulation but none are bifurcate. There is evidence of preservational artifact in papillae; the BFA papillae are compressed flat against the buccal floor, with the lateral papillae pointing away from the midline. Pre-pocket papillae are absent, but there are well developed pustulations in the pre-pocket position on each side of the buccal floor. Anterior to these, above the lateral arms of the ceratohyal, are a few dozen or so tiny papillae and associated pustulations in a diffuse patch. Tiny conical papillae and pustulations are also present in



FIG. 14.—Photographs of the floor (above) and roof (below) of the mouth of a *Leptobrachium hasselti* larva.

abundance on the buccal surface in a triangular area between the BFA, the back of the buccal pockets and the velar surface. The buccal pockets have a nearly transverse orientation: they are wide and deep. They are clearly perforated, although the perforations are not visible without retracting the large folds on the posterior wall of each pocket. The free velar surface is very long; it is supported by long, thin spicules that extend back to the posterior velar margin. The velar margin is nearly straight on each side of the midline, its medial portion is coarsely serrated. There is a well developed median notch bound by two papillae-like projections on each side. The more medial projections are two to three times the size of those immediately lateral. The velum possesses a secondary margin between the branchial baskets ventral to the main edge. This secondary edge also possesses a pair of posterior projections. Large, conspicuous secretory pits of moderate to low density can be found along the middle half of the velar margin. The pits are concentrated on the medial posterior projection.

Ventral pharynx.—The branchial baskets are oval, elongate in the transverse plane, and extremely shallow. All filter cavities are of nearly equal volume, but the filter plates are so short that they effectively form a single common cavity for each branchial basket. The shortening of the filter plates is reflected in an increase in length to height ratios for all the filter plates, particularly those of the second and third ceratobranchials. Counts for filter rows run 5, 8, 9, 6 for cb. 1-4. The values for the first two arches are extremely low while the two other values are within the typical tadpole range. The filter mesh is not dense although the filter rows are all very wide. The wide rows result from longer secondary and tertiary filter folds. Nevertheless, neighboring filter rows do not abut and the filter canals are shallow, 60% canopied by the filters, and about a third as wide as the rows that bound

them. Branchial food traps are completely confined to the horizontal free velar surface; however these surfaces are covered by large, dense secretory pits instead of secretory ridges. These pits completely cover the food traps and can be found on the ventral surface of the ventral velum directly in front of the glottis where they tend to align in transverse rows. The glottis is small, with weakly developed lips; a laryngeal disc is not visible. Ninety per cent or more of the glottis is fully visible when viewed from above but this large exposure may have resulted in part from tissue shrinkage. The esophageal funnel is anteriorly broad but not large.

Dorsal buccal.—The buccal roof is broad overall, but the prenarial arena is narrow. Six pustulations within the narial arena show no particular symmetry. The nares are wide and have a strong transverse orientation. A small pustulate ridge projects from the anteromedial corner of each naris toward the center of the prenarial arena. In the middle of the otherwise low anterior narial walls arise single, tall, attenuate prenarial papillae on each side, matched by equally tall and attenuate narial valve projections of the posterior wall. Both the prenarial papillae and the narial valve projections point away from the narial openings, presumably because of shrinkage. The median ridge is near the nares and the postnarial papillae are in a transverse line between the median ridge and the laterally displaced lateral ridge papillae; consequently, the postnarial arena is shaped much like a transversely elongate oval, two to three times as wide as long. The postnarial papillae are more attenuate than those of *H. regilla* but equally numerous. The median ridge, which lacks a secondary ridge, is small and shaped like a half-circle with fine, evenly spaced, marginal serrations. Lateral ridge papillae are twice as tall as the median ridge. They are narrow, transversely compressed flaps with two attenuate peaks. The

medial peaks are two to three times as tall as the lateral peaks. The buccal roof arena is a well-defined oval bounded by eleven attenuate conical papillae on one side and twelve on the other. Far lateral to the middle of the BRA are clusters of two or three smaller, secondary papillae.

The buccal roof is evenly covered with fine pustulations. In addition, there are larger, more robust pustulations scattered within the BRA. Laterally the glandular zone is of typical length along the anterior-posterior axis but medially it is reduced to a length of only two or three secretory pits. The dorsal velum has been badly distorted from alcohol storage and its full extent cannot be determined. There is a large gap between the left and right halves of the velum and the medial edges—unusual in being papillate—are reflected dorsomedially. I counted seven papillae on each side and roughly an equal number of pustulations.

Dorsal pharynx.—The nature of the pressure cushions could not be determined because of shrinkage. It seems, however, that there is a single cushion that fits into the common filter cavity rather than multiple pressure cushions on each side. The ciliary groove is unusually wide, particularly laterally, but this again may be a preservational artifact.

Diagnostic summary.—See *Oreolalax pingii* (p. 46).

Leptobrachium oshanensis (Liu)

(Fig. 15)

Material.—FMNH 49589 (stage 34, sv. 12.2 mm). Collected from side pools and pools beneath cascades of small streams at approximately 1-1.1 km elevation, Mt. Omei, Szechwan, China; June 15, 1946.

Reference.—Liu, 1950 (p. 199-201).

External.—*Leptobrachium oshanensis* larvae have an enlarged oral disc (like many stream tadpoles) but much of it is denticle free. The usual pattern for denticle rows is 4/3, but it is not

uncommon for there to be one row more or less above or below. The spiracle is sinistral; the body and tail are elongate.

Ventral buccal.—The lower beak is larger and positioned more dorsally in *L. oshanensis* than in *L. hasselti*. The floor of the mouth is of typical width and not as broad as in *L. hasselti*. Very large, hand-like infralabial papillae are present; like many other oral papillae, they show a tendency to be divided into long, secondary papillae. The infralabial papillae are tall structures with a half-dozen or more extremely attenuate, pointed "fingers" that arch anterad. There are two rather than three papillae on each side anterior to the infralabial papillae. The more anterior papillae are the larger. These are flattened into the transverse plane, bifurcated and are pointing out of the mouth. The papillae between these and the hand-like papillae are small, simple projections. The two medial papillae, which were noted as possible anteriorly displaced lingual papillae in *L. hasselti*, are taller in *L. oshanensis* and also project anteriorly. Papillae are absent from the tongue anlage. On each side, laterally adjoining the tongue anlage, are small, oval swellings; on the top of these swellings are one or two moderate sized attenuate papillae. The buccal floor arena differs from that of *L. hasselti* in being fully open posteriorly. The BFA papillae rows converge slightly both anteriorly and posteriorly, giving the arena a typical oval design. While BFA papillae are as numerous as in *L. hasselti*, they are taller and even more attenuate. Three BFA papillae on one side and four on the other have terminal divisions. The papillae in the middle of the series are much larger than those in the front or back of the rows. There are one or two small, conical spikes in the pre-pocket positions. These are at the back of a short row of similarly shaped papillae that extend in a line anteromedially over the lateral arms of the ceratohyals. *L. oshanensis* lacks the papil-

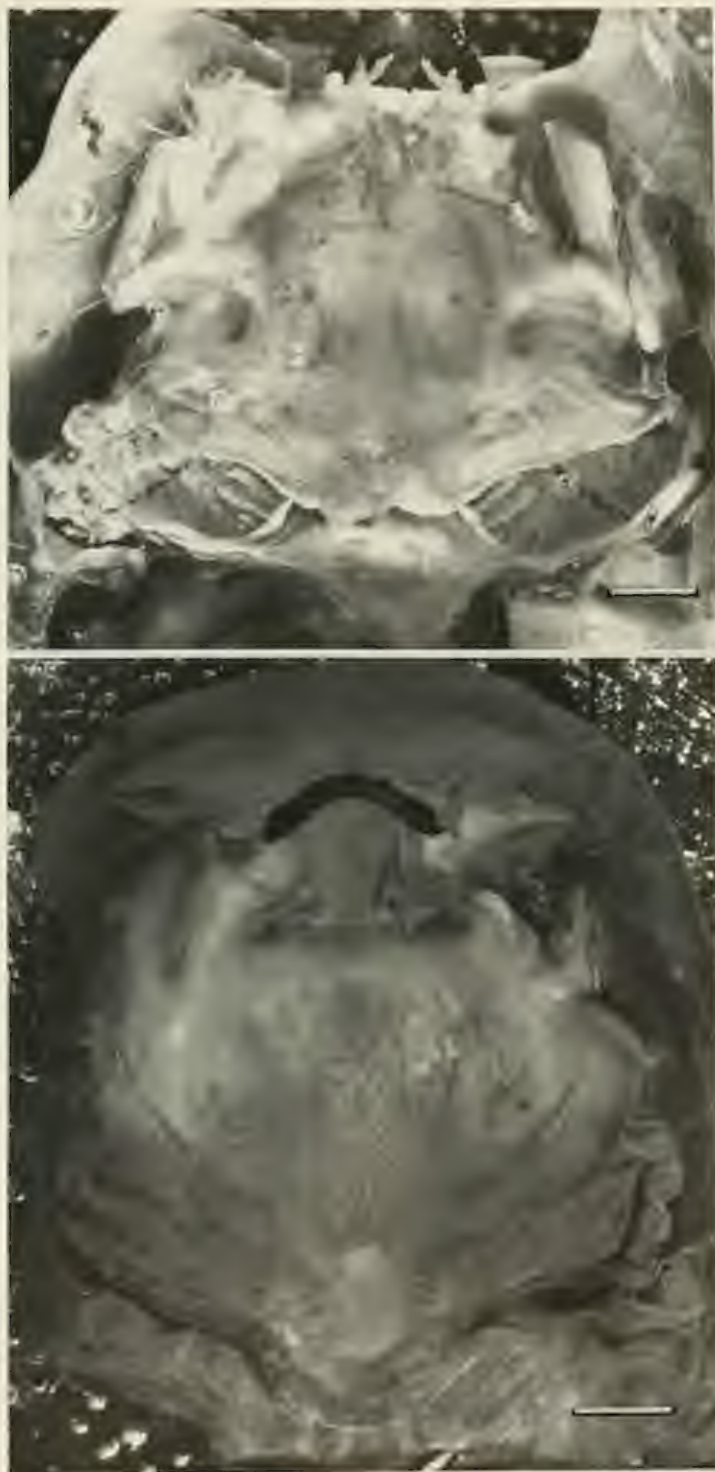


FIG. 15.—Photographs of the floor (above) and roof (below) of the mouth of a *Leptobrachium oshanensis* larva.

late patches seen in *L. hasselti* in front and behind the buccal pockets. There is, however, a relatively dense field of stiff, conical pustulations within the posterior half of the buccal floor arena not seen in the other species. These pustulations extend farthest forward on the midline to about the level of the buccal pockets. Posteriorly, they reach the velar margin and generally increase in size as one goes backwards over the buccal floor. The buccal pockets are longer and not as wide as in *L. hasselti*. The bottoms of the pockets are fully obscured by massive folds from the posterior walls. I could not find clear natural perforations. The free velar surface differs from that of *L. hasselti* in having weak posterior projections rather than medial crenulations over the filter cavities and in having a uniform, narrow, but thickened band of secretory pits along its posterior margin. A deep median notch is bound by massive brushes of extremely attenuate papillae. These arise from a double—dorsal and ventral—medial edge on the ventral velum, as in *L. hasselti*. The numerous papillae are preserved in an anteriorly folded direction in this specimen.

Ventral pharynx.—The branchial baskets are smaller than in *L. hasselti*. The filter plates have even less height. Counts for filter rows run 7, 10, 8, 5 for cb. 1-4. These values are below the mean for *H. regilla*, but none significantly. The values for cb. 1 and 2 are actually above the values for *L. hasselti*; this is possible within the smaller branchial baskets of this species because the filter rows are narrower. Filter canals are slightly more open in *L. oshanensis* than in *L. hasselti*. As with *L. hasselti*, the branchial food traps are covered with secretory pits rather than ridges and the pits are continuous across the ventral surface of the ventral velum and in front of the glottis. The glottal lips are larger in this species than in *L. hasselti* and the glottis is fully exposed within the median notch. There are two

tiny anterior papillae on the glottal lips. The laryngeal disc is visible as a very wide, transversely oriented, oval ridge. The esophageal funnel is of comparable size and proportions in the two species.

Dorsal buccal.—The roof of the mouth has roughly the same proportions as in *L. hasselti*. The upper beak is reflected posteriorly in *L. oshanensis*, obscuring about 40% of the prenarial arena from ventral view. The number of pustulations in the prenarial arena is reduced. The prenarial papillae and narial valve projections are not quite as tall as in *L. hasselti*, but are still far taller than in any hyliid. The narial valve projections are displaced slightly laterally. The median ridge is farther posterior and the postnarial arena is larger than in *L. hasselti* but not as large as in a typical tadpole. The positions of the postnarial papillae are as in *H. regilla*, not as in *L. hasselti*. The median ridge and lateral ridge papillae are similar to those of *L. hasselti* except for being slightly taller and wider. The papillae that define the buccal roof arena are like those of *L. hasselti* in number and position, but more attenuate in *L. oshanensis*. The largest papillae are anterior. The papillae in the clusters lateral to the BRA are more numerous in this species. The BRA encloses a field of stout conical pustulations, which are very large, stiff, subpapillate structures of only moderate density at the front of the arena. Posteriorly, the pustulations become both smaller and more numerous. The pustulate field ends in a transverse line that laterally abuts with the glandular zone; the glandular zone is broadly interrupted medially. The dorsal velum is also interrupted in front of the esophagus but the gap between the left and right portions of the glandular zone is twice the width of the gap between the left and right halves of the velum. Secretory pits within the glandular zone are similar in both species. The dorsal velum is generally short; it is anchored on each side of the roof just

behind the medial limits of the glandular zone. Although it is a free flap both lateral and medial to these points, the medial portions of the dorsal velum are relatively immobile. The medial portions of the velum are turned backwards and are lined with long, attenuate papillae, twice as many as in *L. hasselti*. Papillae in this general region are not restricted to the margin of the velum; they are also prevalent on the pharyngeal surface of the velum and on the buccal roof above the medial edges of the velum.

Dorsal pharynx.—The lateral and medial pressure cushions are completely confluent. The ciliary groove is very wide and shallow.

Diagnostic summary.—See *Oreolalax pingii* (p. 46).

Oreolalax pingii (Liu)

(Fig. 16)

Material.—FMNH 50988 (stage 36, sv. 25.8 mm). Collected among stones in slow-running streams at approximately 2.7-3.4 km elevation, between Hsuan-shenpa and Lolokou (N. 28°0', W. 102°30') on the road between Sichang and Chaochiao, Sikang, China; May, 1942.

Reference.—Liu, 1950 (p. 149-150).

External.—*O. pingii* tadpoles have an invariant 5/5 denticle pattern. The spiracle is sinistral. In general appearance they are similar to *Leptobrachium* larvae. In terms of tail length *O. pingii* larvae are intermediate between *L. hasselti* and *L. oshanensis*. Internally *O. pingii* larvae are sufficiently similar to the two species of *Leptobrachium* described above that comparison with those species is emphasized in the following description.

Ventral buccal.—The buccal floor is more triangular than in either species of *Leptobrachium* and the prepocket portion is relatively longer. The infralabial papillae are most similar to those of *L. oshanensis*. They differ in being overall smaller and in being covered by large, pointed pustulations. All but the small-

est buccal papillae in *O. pingii* have this unusual pustulate surface. The most anterior infralabial papillae are very stout and are divided into four or more projections. Smaller papillae between the main infralabial papillae and the anterior pair are absent. The medial pair of infralabial papillae, between the main infralabial papillae, are very tall and have two or more terminal subdivisions. As in *Leptobrachium*, the lingual anlage lacks papillae. The buccal floor arena is similar to that of *L. oshanensis*; the BFA papillae are a bit larger. The largest BFA papillae are fused basally with their neighbors. Papillae in the prepocket position and over the lateral arms of the ceratohyals are like those of *L. oshanensis* in position and shape. Papillate patches are present directly behind the buccal pockets as in *L. hasselti*, although they are not as numerous as in that species. The pustulate field within the BFA is more similar to that of *L. oshanensis* than that of *L. hasselti*, but differs from the former in extending farther forward on the midline and being made up of overall smaller, blunter, and less dense pustulations. The far posterior portion of this pustulate field has the smallest pustulations and the greatest density. The buccal pockets are intermediate between those of *L. hasselti* and *L. oshanensis* in all aspects that have been considered; there is a definite small perforation of the pockets in this species. The free velar margin is supported by thicker spicules in *O. pingii* than in either species of *Leptobrachium*. There are three distinct small, round, posterior projections of the velar margin on each side. These are similar in position to those of *H. regilla* but more distinct. The median notch and the two projections that immediately bound it are a bit larger than in *L. hasselti*, but otherwise similar. The odd, secondary, ventral edge to the medial portion of the velar margin—characteristic of both species of *Leptobrachium*—is rudimentary in *O. pingii*. On the ventral side of the

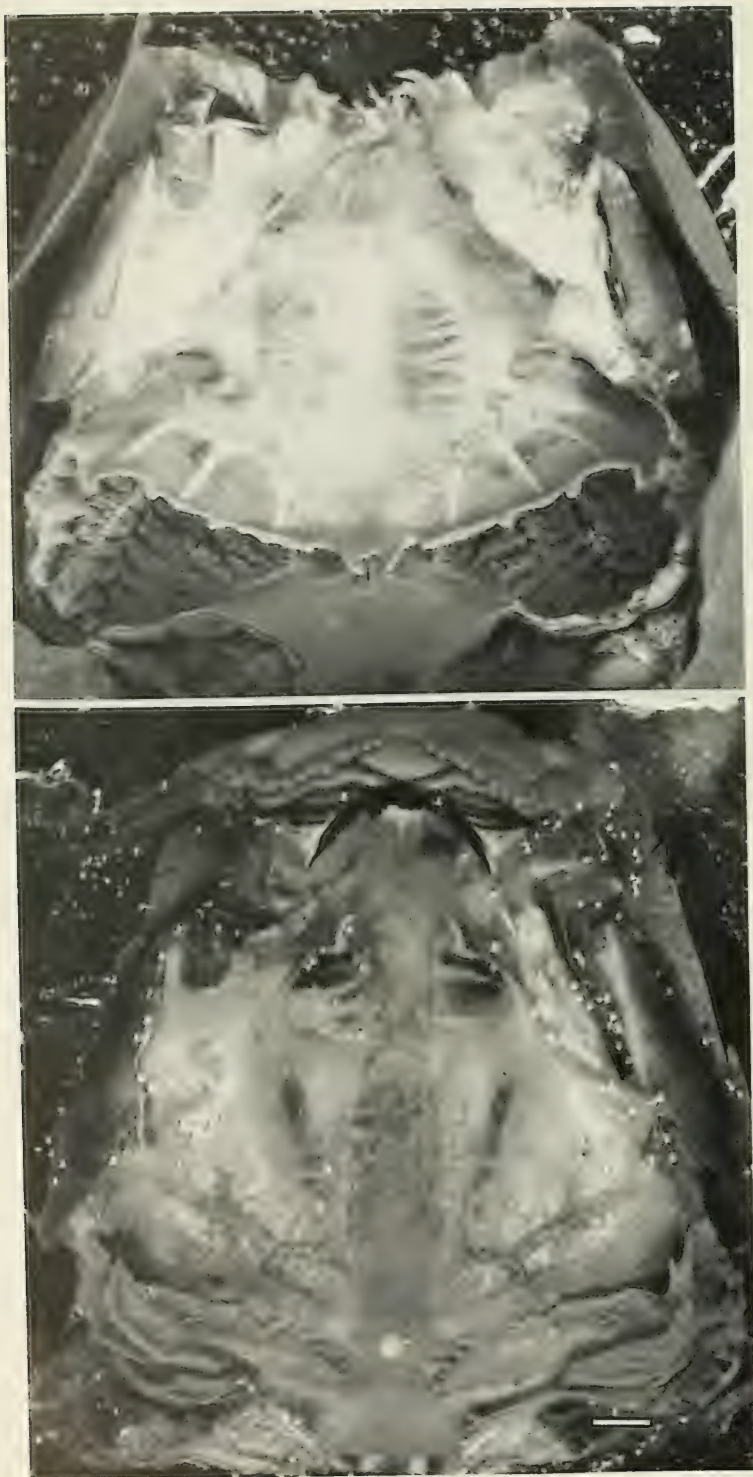


FIG. 16.—Photographs of the floor (above) and roof (below) of the mouth of an *Orcolalax pingii* larva.

medial portion of the velar margin are four small, simple, posteriorly directed papillae. The lateral pair are the largest, but are still too small to reach the velar margin and be seen from above. Secretory pits on the velar margin are as in *L. oshanensis*.

Ventral pharynx.—The branchial baskets of *O. pingii* resemble those of *L. hasselti* in shape; they are intermediate between those of the two species of *Leptobranchium* in relative size. Essentially there is only one common filter cavity in *O. pingii* larvae on each side; for it is only far forward, under the velum, that the filter plates of any ceratobranchial is as tall as its filter rows. Counts for filter rows are identical to those of *L. oshanensis*. No characters of the filter themselves serve to distinguish the filters of *O. pingii* from those of *L. oshanensis*. Secretory pits could be found only on the ventral surface of the ventral velum. In that regard, *O. pingii* is no different from the species of *Leptobranchium*. In terms of the pattern of the pits in front of the glottis, the glottis itself, and the esophageal funnel, *O. pingii* is indistinguishable from *L. hasselti*.

Dorsal buccal.—The buccal roof is more triangular in *O. pingii* than in either species of *Leptobranchium*. In size and proportions the prenarial arena is intermediate between that of the two species of *Leptobranchium*. There are two tall, but simple, cylindrical papillae positioned far laterally within the prenarial arena. These project ventrally between the main infralabial papillae and the anterior infralabial pair. The internal nares are most similar to those of *L. hasselti*. They differ in the following ways: the anterior walls are pustulate (and there is a second prenarial papillae on one side in this specimen); the narial valve projections are not as tall. The median ridge is more posterior in *O. pingii* than in either species of *Leptobranchium*, but still semicircular in shape. Marginal serrations are very coarse. The median ridge has a pustulate anterior

surface, but lacks a secondary ridge. The postnarial arena is average in size. Postnarial papillae (four per side) are positioned in oblique clusters as in *H. regilla* and *L. oshanensis*. These papillae are larger than in *L. oshanensis*, the largest being the most posterolateral. All have serrated anterior margins. The lateral ridge papillae are huge, flap-like structures positioned far lateral as in *Leptobranchium*, but much larger than in that genus, and with three, rather than two, terminal projections. The BRA of *O. pingii* is anteriorly narrower, but posteriorly wider, than that of *L. oshanensis*. Within the arena proper is a field of two to three dozen small to medium sized papillae, most of which have terminal pustulations. A small, triangular cluster of papillae extends laterally from the posterior portion of the BRA. The dimensions of the glandular zone are most comparable to those of *L. hasselti*. The zone differs, however, from either species of *Leptobranchium* in having extremely large and conspicuous secretory pits along its anterior margin. The dorsal velum is shorter than that of *L. oshanensis* and interrupted medially. The anterior margin of the velum is nearly transverse except in the neighborhood of the midline, where it is reflected posteriorly. Papillae are present along the medial half of the velar margin. These are as numerous as in *L. hasselti* and intermediate between those of *L. hasselti* and *L. oshanensis* in size.

Dorsal pharynx.—A single, transversely elongate pressure cushion is present on each side. These cushions extend from the lateral margin of the pharynx halfway to the medial margins of the dorsal velum. Their shorter, anterior-posterior axes are a quarter or less the length of their longer, transverse axes. The cushions have indented anterior and medial margins, which give them an autonomy from the dorsal velum not seen in any other tadpoles. The ciliary groove is similar to that of *Leptobranchium*.

Diagnostic summary.—The non-*Megophrys* megophrynines form a tight cluster of species that share the unique character of having multiple, layered papillation of the medial portion of the ventral velar margin. They also tend to have extremely tall prenarial and postnarial papillae and papillation of the medial margin of the dorsal velum. *Leptobranchium oshanensis* can be distinguished from *L. hasselti* by an assortment of minor characters. The most conspicuous of these includes the size of the infralabial papillae and extent of papillation of the medial margins of the dorsal and ventral vela. *Oreolalax* can readily be distinguished from the species of *Leptobranchium* examined by the unusual pustulation of its buccal papillae.

HYLIDAE

Anotheca spinosa Steindachner

(Figs. 17, 18)

Material.—KU 60017 (stage 37, sv. 14.5 mm). Collected in tree hole containing approximately 60 ml of water at 1600 m elevation, Vista Hermosa, Oaxaca, Mexico; August 12, 1960.

Reference.—Duellman, 1970 (p. 149-150).

External.—*Anotheca spinosa* has stout, muscular larvae with very broad beaks and a 2/2 denticle pattern in early stages. The upper rows of denticles tend to disintegrate in later stages. The spiracle is sinistral.

Ventral buccal.—The floor of the mouth in the frontal plane is roughly an equilateral triangle. Two distinct pustulations are aligned directly behind the keratinized beak on each side. Behind these and about halfway between the symphysis and the articulation of the infralabial cartilage with Meckel's cartilage is an infralabial papilla on each side; the papillae are shaped like slightly compressed cylinders and point anterodorsally. Secondary, stubby, terminal projections on the papillae number five on one side and four on the other. There

is only one lingual papilla in this specimen. It is terminally bifurcated and laterally expanded, and looks much like two normal papillae that have fused on the midline. The buccal floor arena is very broad. The lateral row of papillae outlining the arena converge little toward the midline at either the front or the back of the arena. The BFA papillae are average in number, but shorter and blunter than in typical hylids. The larger papillae, i.e., those in the posterior half of the arena, are flattened against the floor of the cavity and directed out away from the midline rather than medial as in most other tadpoles examined. This unusual orientation may, in part, result from shrinkage following preservation. The two largest BFA papillae on each side have terminal bifurcations. Some three dozen small, blunt pustulations and tiny papillae are scattered about in the posterior half of the BFA. A half dozen similar projections are above the lateral arms of the ceratohyal outside of the arena. The buccal pockets are short, slender, and more obliquely oriented than those of a typical hylid; they are not perforated. The free velar surface is very much reduced. Supporting spicules are thin and short. The posterior margin of the velum is predominantly transverse with very faint crenulations projecting posteriorly over the first two filter cavities. The shallow median notch is so broad that it covers no less than half of the velar edge. Secretory pits could not be found on the margin and are likely absent.

Ventral pharynx.—The branchial baskets are greatly reduced. The filter plates are reduced in all directions, although they still retain some height. Vestiges of filter rows are present as thin, irregular folds of epithelium. These number 3, 3, 3, 2 for cb. 1-4. Only the main folds are present. The filter canals are completely open and two to four times as wide as the vestiges of the filter rows. Branchial food traps are absent; that is, no organized secretory ridges could be resolved

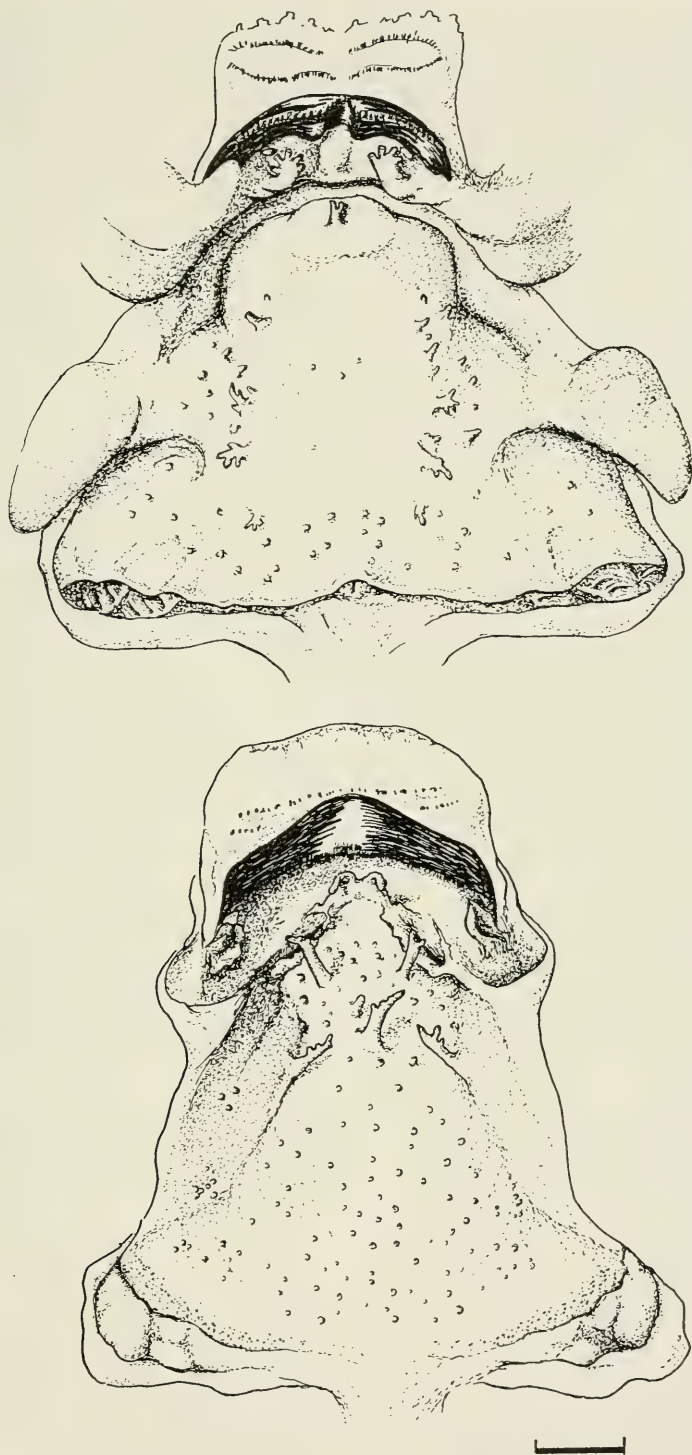


FIG. 17.—Drawings of the floor (above) and roof (below) of the mouth of an *Anotheca spinosa* larva.

anywhere in the pharynx. The glottal slit and lips are large and vertically oriented. They are 50% under the velar margin. The glottis sits on a large, gently domed, laryngeal disc. The esophageal funnel is of enormous width and extremely broad profile.

Dorsal buccal.—The roof of the mouth shares the equilateral triangular shape of the floor of the mouth. The lateral margins of the roof, however, curve downward more than in other tadpoles examined, giving the roof considerable depth. The internal nares and median ridge are far forward on the buccal roof. The prenarial arena is twice as broad as long. Two tall, knobby projections with blunt apices arise from the middle of the prenarial arena. The tips of these projections are turned posteriorly. The stout common pedestals for these projections bow forward on the midline and extends back on each side as ridges that become continuous with the posterior wall of the internal nares. The internal nares are shallow slits, more elongate and oblique than in a typical hylid larva. The far anteromedial corners are pustulate flaps. Anterior walls are effectively absent except laterally where there are some blunt pustulations and a distinct, pustulate, prenarial papilla on each side. The posterior narial walls each have a slight to moderate narial valve projection, but the projections are in the middle rather than at the anteromedial end of the posterior wall. There is a deep groove that separates the posterolateral portion of the posterior narial wall from the postnarial arena on each side. It is not clear whether the posterior narial walls of *A. spinosa* tadpoles would be efficient as valves. The postnarial arena contains two tall, straight papillae that project anterolaterally under the narial valve projections. These have pustulate apices and some sign of terminal bifurcation. The median ridge is reduced to a tall papilla with an expanded base and a pustulate anterior margin. It is com-

pressed in the sagittal plane and collapsed asymmetrically against the buccal roof in this specimen. Anterolateral to the median (ridge) papilla and within the postnarial arena are fifteen to twenty pustulations and a single, simple papilla. Posterolateral to the median (ridge) papilla are two typical lateral ridge papillae. The buccal roof is devoid of any papillae that could outline a buccal roof arena. A hundred or more blunt pustulations, including a few stubby subpapillate projections, cover the buccal roof proper. I could not resolve a glandular zone. The dorsal velum is completely absent.

Dorsal pharynx.—Without a dorsal velum the buccal and pharyngeal roofs are completely confluent. There are no pressure cushions.

Diagnostic summary.—*Anotheca* larvae are uniquely different from all other tadpoles examined in the following features: single medial lingual papillae; gigantic median notch and ventral velar margin; filter rows reduced to thin, single folds; dorsal velum and dorsal pharyngeal features absent.

Gastrotheca riobambae (Fowler)
(Fig. 19)

Material.—Author's collection (stage 37, sv. 20.6 mm). Laboratory raised; Mus. Nat. Hist. Univ. Kansas.

References.—Hoogmoed, 1967; Duellman, 1974.

External.—*G. riobambae* larvae are large, with dorsolateral to nearly dorsal eyes, a 2/3 denticle formula, and sinistral spiracle. Tadpoles of this species are often known under the name *Gastrotheca marsupiata* (see Duellman and Fritts, 1972 and Duellman, 1974, for the most recent discussion of the systematics of the genus).

Ventral buccal.—The width to length ratio for the mouth is typical for a hylid tadpole but the floor is noticeably rounder than in most species examined. There are four infralabial papillae in a transverse line. The medial pair consists of

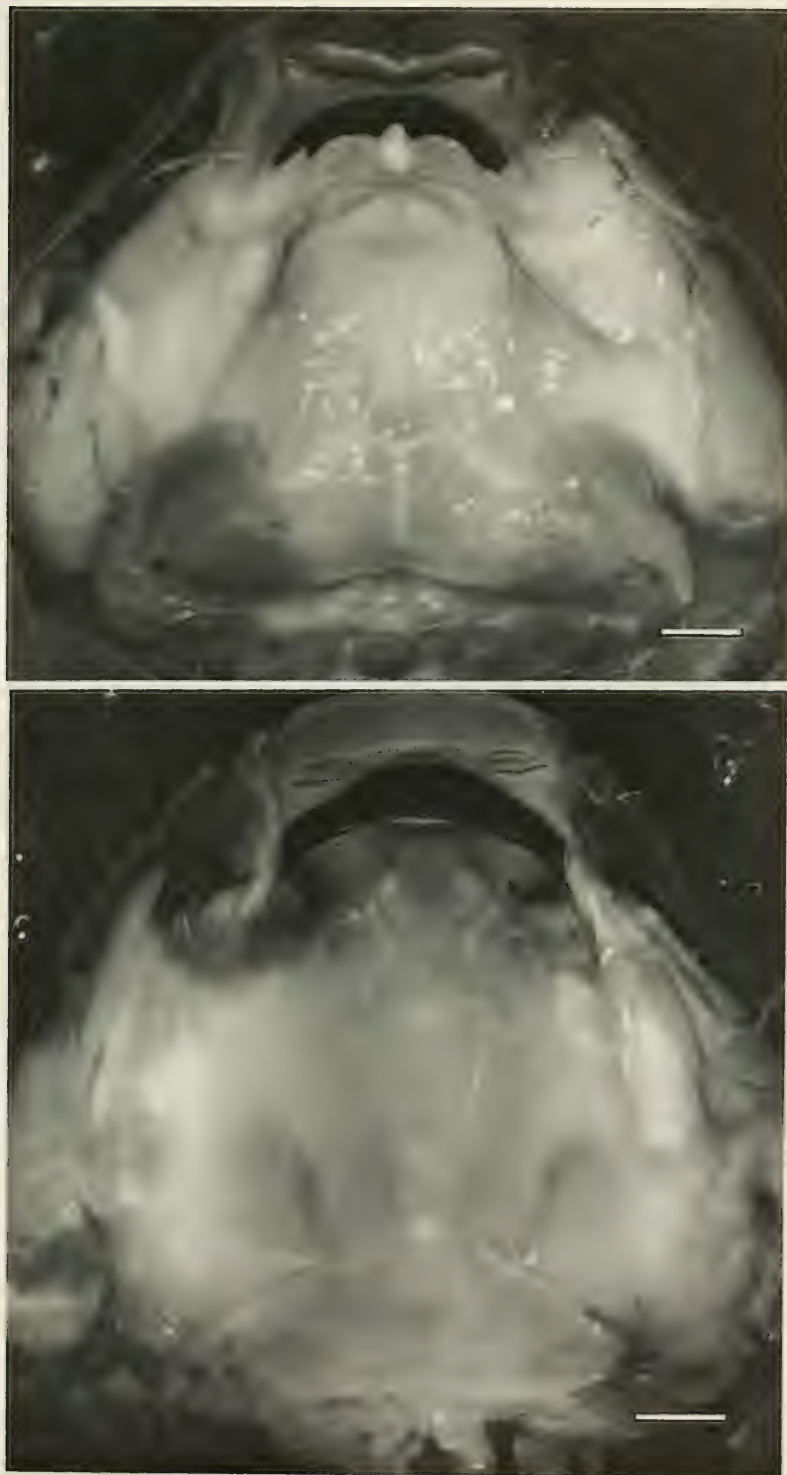


FIG. 18.—Photographs of the floor (above) and roof (below) of the mouth of an *Anotheca spinosa* larva.

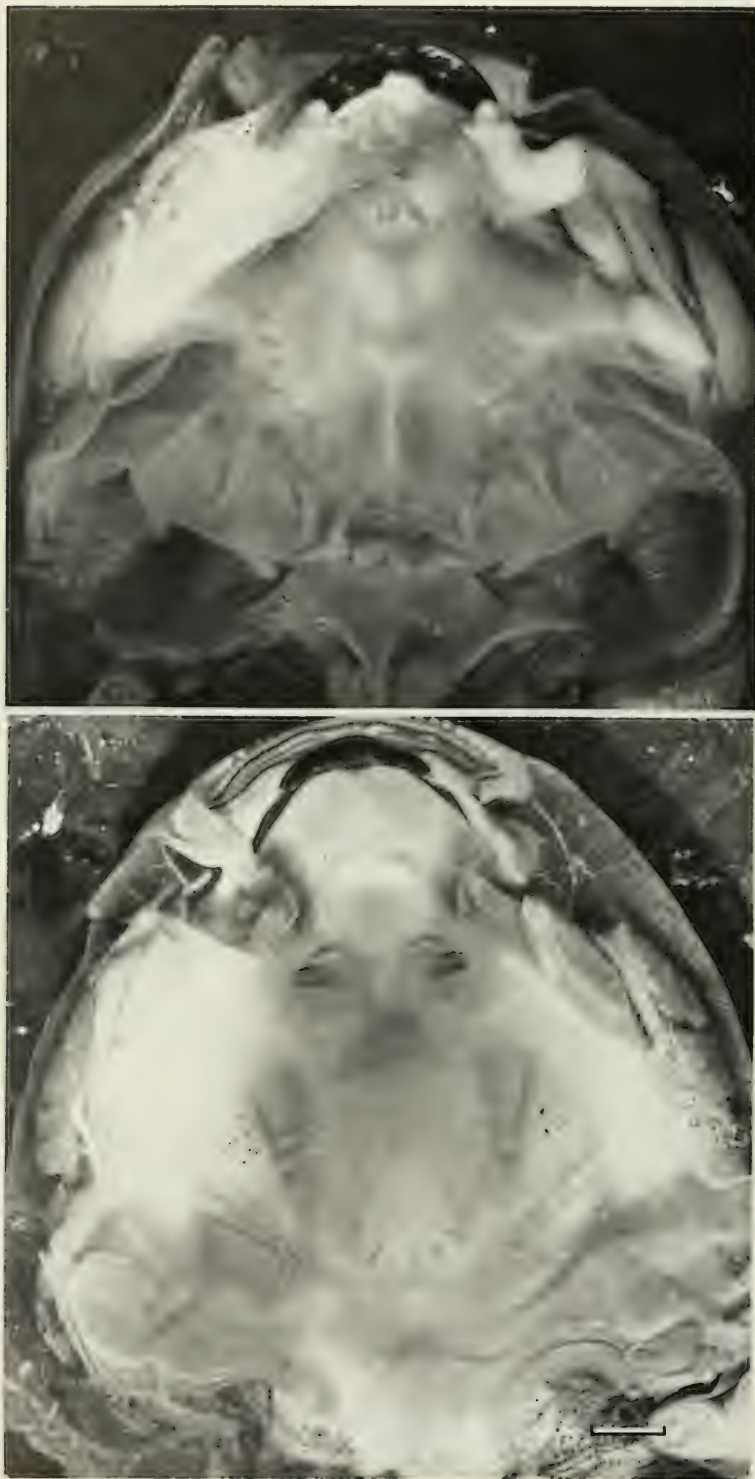


FIG. 19.—Photographs of the floor (above) and roof (below) of the mouth of a *Gastrotheca riobambae* larva.

moderately tall, finger-like projections. The lateral two are shorter and may be considered bipartite. On each side dorsal to the infralabial papillae, in the angle between the upper and lower beaks, is a small, but distinct keratinized spur. These spurs are directed anteriorly and separate from the main keratinized beaks. They are just far enough back inside the mouth so that they cannot contact a smooth substrate when the lower jaw is fully depressed. *G. riobambae* has four lingual papillae. The two tallest are near the midline; the other two are slightly shorter and posterolateral to the medial pair. The buccal floor arena is wide. The BFA papillae series is continuous posteriorly across the midline. I counted 17 BFA papillae on one side, 19 on the other; only nine rather small BFA papillae are anterior to the buccal pockets. The papillae behind the pockets are not in tight rows but spread out laterally to cover the region of the buccal floor between the median ends of the buccal pockets and the front of the second filter cavity. The four largest papillae, viz. those just medial to the buccal pockets, show basal bifurcation; a few of the other larger papillae have minor pustulations along their sides. Posteromedially within the arena is a pair of small papillae. There are also about sixty tiny, faint pustulations randomly dispersed within the caudal two-thirds of the arena. *G. riobambae* has typical pre-pocket papillae. The buccal pockets are wide, with a strongly oblique orientation. The pockets are shallow and perforated. The free velar surface is long, supported by spicules; the posterior projections of the velar margin are also long. The projections associated with the third filter cavity are displaced medially. All pairs of projections are directed postero-medial. The single pair of projections surrounding the median notch are thicker than the rest of the velar surface; they are directed dorsad because the mid-portion of the velar margin is forced

forward by a relatively gigantic laryngeal disc. The projections are covered with dense, conspicuous secretory pits.

Ventral pharynx.—The branchial baskets are long and deep. The baskets overall have a more circular, rather than typically oval, dorsal profile. This shape seems to reflect modifications of the third filter cavity. The tiny, third filter cavity, as viewed from above, is a nearly closed chamber capped by the imbricating, curved dorsal margin of the filter plate on cb. 3. Filter plates of cb. 1 and cb. 2 are relatively long; plates of cb. 3 are exceptionally tall. Counts for filter rows are very near the mean for *H. regilla*, but filter rows are wider with longer secondary folds. Filter canals are of typical proportions. Filter rows at the bottom of the plates lining filter cavities 1 and 2 are fused, not only with neighboring rows on each plate, but with the abutting filter rows of the opposing plate. Thus, the gill slits are completely obscured from dorsal view and water that enters those two filter cavities must pass through individual filter niches in order to reach the atrial chamber. The branchial food traps of *G. riobambae* cover a disproportionately large area in the anterior portions of the filter cavities. Secretory ridges are of greater absolute size and height than in a typical hyliid tadpole, but whether this difference is significant could not be determined. While the glottal slit and glottal lip proportions are not unusual, the glottis in *G. riobambae* differs from most other tadpoles examined in having a predominantly vertical orientation. The glottis sits on a huge, but not very conspicuous laryngeal disc. *G. riobambae* has esophageal funnel of very broad profile.

Dorsal buccal.—The roof of the mouth of *G. riobambae* is broad anteriorly and quite round. The nares and median ridge are positioned far back on the buccal roof, resulting in relatively large pre- and postnarial arenas. The caudal half of the large prenarial arena is filled by a gentle, upside-down, U-

shaped depression of the rostrum. Pustulations are absent within this arena. The internal nares are transversely oriented, quite small, and nearly as wide as long. The walls, particularly the medial portion of the anterior wall, are very thick. Pustulations are few and faint on the anterior wall; prenarial papillae are absent. Narial valve projections are very slight. A deep groove separates the posterior narial wall from the postnarial arena. Postnarial papillae are typical in position and number, although with pustulate anterior margins. The median ridge is not unusual in shape or marginal sculpturing, but lacks pustulations or a secondary ridge on its anterior surface. Within the postnarial arena are three or four tiny, blunt papillae. One is located medially in the anterior half of the arena; the remaining ones are aligned transversely just in front of the median ridge. The lateral ridge papillae are slightly compressed into the sagittal plane. They are bifurcate, with shorter anterior and taller posterior projections, and have very tiny pustulations on their anterior surfaces. The BRA is well defined—oval in shape with a truncated anterior margin—by a continuous arc of no less than 16 papillae. These papillae are simple and moderate in size. In general, BRA papillae are evenly spaced in single file; however, in the posterolateral margins of the arena there are one or two small secondary papillae neighboring the main row. Fifty to one hundred small, pointed pustulations are randomly dispersed within the arena. Three or four small, pointed papillae may be found clustered along the far lateral margins of the buccal roof. The glandular zone of *G. riobambae* is narrow and tends to be of a uniform width across the buccal roof. Secretory pits are very conspicuous and large, as were the secretory ridges in the ventral pharynx; the apparent accentuation of larval secretory tissue in this species, however, may not be significant when overall size is taken into account. The

dorsal velum is average or a bit larger than average for a hyliid tadpole; the gap between the left and right sides of the dorsal velum is great.

Dorsal pharynx.—*G. riobambae* has two large and conspicuous pressure cushions, obliquely oriented on each side. The lateral cushions are the larger and rounder, and the medial cushions are of subequal width to the lateral pair. The ciliary groove is not noticeably different from that of any typical hyliid larva.

Diagnostic summary.—*Gastrotheca riobambae* has: ventral fusion over the gill slits of the filter rows from neighboring filter plates; a medially directed spur on each side at the front of the mouth and four lingual papillae. Cursorial examination of larvae from other *Gastrotheca* species (*G. monticola*, KU 142847, N = 1, stage 35; *G. marsupiata*, KU 139442, N = 4, all stage 36) suggest that these features characterize the genus not the species. In *G. marsupiata* the fusion of the filter rows, however, is incomplete in the posterior portion of the filter cavity.

Hyla femoralis Sonnini & Latreille
(Fig. 20)

Material. — Uncatalogued, author's collection (stage 36, sv. 16.0 mm). Collected from small pond, 1.25 km NE Florida Technical Univ., Orange Co. Florida; August 12, 1975.

Reference.—Wright, 1932.

External.—This is possibly the most beautiful tadpole in North America. This specimen has a tall tail fin, which is almost as tall as it is long, and ends in a pointed flagellum. The denticle pattern is 2/3; the spiracle is sinistral.

Ventral buccal.—*H. femoralis* is so similar to *H. regilla* that only differences are emphasized in this description. The floor of the mouth is slightly broader posteriorly in *H. femoralis* than in *H. regilla*. The infralabial papillae are smaller and narrower. The lingual papillae are positioned far forward and

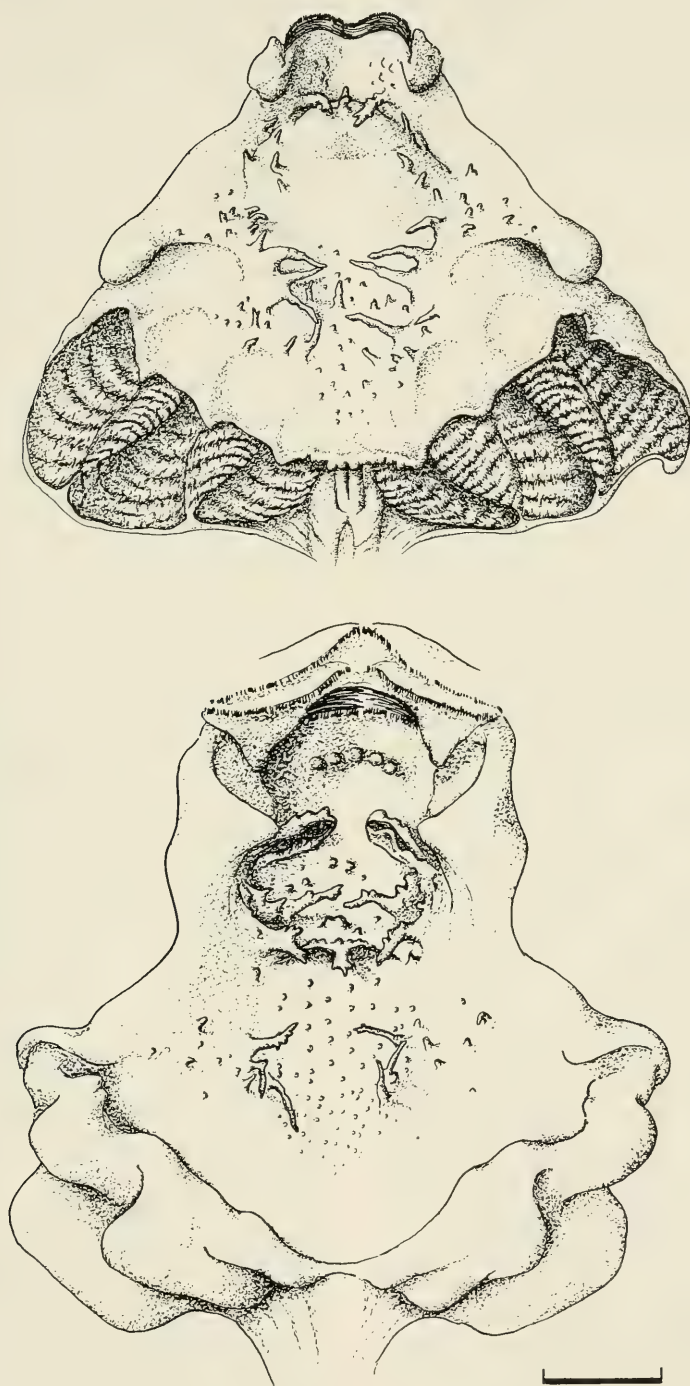


FIG. 20.—Drawings of the floor (above) and roof (below) of the mouth of a *Hyla femoralis* larva.

almost touch the infralabial papillae. The buccal floor arena is an oval area well defined by 11 papillae on one side, eight on the other. The two to three largest papillae on each side, those directly medial to the buccal pockets, arise from a common ridge-like base. Approximately 20 pustulations occur in the posterior half of the BFA. Four to six large pustulations/subpapillate structures are dispersed on the buccal floor anterior to the buccal pockets. The buccal pockets are shallow. The floor of each pocket is completely obscured by a large fleshy fold from its dorsal wall. Any perforation of the floor of the buccal pockets must be relatively small and very medial. The free velar surface is slightly longer than in *H. regilla*.

Ventral pharynx.—The branchial baskets are larger than those of *H. regilla*. The posterior margin of the baskets are elongated, reflecting elongation of the second and third filter plates. The second and particularly the third filter plates are noticeably taller in this species. The third filter plate has an arched dorsal margin which curls medially and nearly completely covers the third filter cavity. Filter counts cb. 1-4 were: 11, 11, 14, 17; these are all well above the counts for *H. regilla* at any stage. Filter rows abut completely; the filter canals are narrow and hidden from view. The filters have a fully developed mesh made up of secondary, tertiary and higher order filter folds. Among the hylids examined only *Agalychnis* had a filter mesh that was denser. Branchial food traps are necessarily large, covering the ventral surface of the ventral velum and much of the anterior region of each filter cavity. A pattern of well organized secretory ridges could be observed on the underside of the ventral velum. The glottis is of average size and only a quarter covered by the margin of the ventral velum. The lips are slightly heavier than those of *H. regilla*. The esophageal funnel is narrow.

Dorsal buccal.—The buccal roof is

indistinguishable in shape from that of *H. regilla*, except that the dorsal pharyngeal region is longer. In the center of the prenarial arena descends a bulge approximately twice as wide as the minimum distance between the internal nares. The bulge has a distinctive anterior arched margin which is lined with a half-dozen blunt pustulations (similar structures are seen in *Smilisca sordida*). The internal nares are identical to those of *H. regilla* in proportion, shape, orientation and valvular structure. The prenarial papillae however are smaller than those of the average *H. regilla*. The median ridge is small and has a pustulate irregular margin. Two large papillae with strongly pustulate edges lie halfway between the median ridge and the internal nares. Smaller papillae arise from the base of these large papillae on their anteromedial side. There are two large pustulations in the anterior portion of the postnarial arena and a large bicusped subpapillate projection in the middle of the posterior part of the postnarial arena. There is a large, flap-like, laterally compressed, irregularly shaped projection in the typical position of the lateral ridge papillae on each side. The buccal roof has three distinct papillae on each side arranged in an oblique row (anterolateral to posteromedial). These define the lateral bounds of the BRA. There is a single tiny papilla located far laterally on the buccal roof. Approximately fifty pustulations are distributed between the median ridge and the posterior quarter of the BRA. The more posterior pustulations are smaller and more numerous. Three to four pustulations occur on the buccal roof lateral to the BRA. The glandular zone is relatively narrow and slightly longer laterally than medially. It is made up of large distinct secretory pits. The dorsal velum is of comparable size to that of *H. regilla*. It is barely continuous across the midline.

Dorsal pharynx.—The pressure cushions are large obliquely oriented swell-

ings. The lateral pressure cushion is the larger. The medial pressure cushion has itself a medial swelling presumably a pressure cushion for the third filter cavity. The ciliary groove is a large open trough.

Diagnostic summary.—The oral cavity of *H. femoralis* is very similar to that of *H. regilla* but can be distinguished from the latter species by larger branchial baskets, taller filter plates and denser gill filters. Papillation and pustulation is slightly more extensive in *H. femoralis* than in *H. regilla*.

Hyla rufitela Fouquette

(Figs. 21, 22)

Material. — Uncatalogued; author's collection (stage 36, sv. 15.4 mm). Collected in grassy pools on the edge of the town Rincon de Osa, Puntarenas, Costa Rica; March 3, 1970.

Reference.—Duellman, 1970 (p. 243-244).

External.—This tadpole is proportioned like most "generalized" hyloid larvae. The spiracle is sinistral. These tadpoles are otherwise unusual in having a 2/4 denticle pattern.

Ventral buccal.—The interior of the mouth has a rounded appearance though the width to length ratio for the oral floor is average. This species has supernumerary infralabial papillae, eight per side in the specimen at hand. Of the eight, three are far anterior, stubby, blunt and with auxiliary pustulations; these form a transverse row on each side. The largest of the three is nearest to the midline. Immediately behind the middle of these is a wide, blunt papillae of medium size. Posterior to this are three compressed papillae with jagged margins which form a second transverse row. The middle papilla of this posterior row is of the same size as the papillae in the front row; the other two are much smaller. The last infralabial papilla on each side is behind the second row, and it is the largest of all eight papillae. Topographically the most pos-

terior papilla on each side appears to be the homologue of the infralabial papilla in species that have only one per side. This papilla is a large, transverse, slightly conical fan. It has a constricted base and strongly papillate margin. The secondary marginal papillae, numbering four and six per side, are further decorated with yet finer jagged projections. The BFA is demarcated by many small papillae and pointed pustulations. In addition to having papillae outlining an ovoid BFA, a transverse row of papillae above the junction of the ceratohyals and hypobranchial plates splits the arena into anterior and posterior portions. I counted thirteen BFA papillae on one side and fifteen on the other. Little weight can be given these counts, however, because of great difficulty in assessing what is a "miniscule papilla" versus a "subpapillate pustulation" in this particular species. Larger projections that are unquestionably of "papilla" proportions tend to be small, compressed cylinders; three had terminal bifurcations. The largest papillae are in the transverse row and pointed anteriorly. The concentration of pustulations and papillae elsewhere on the buccal floor, including lingual papillae and pre-pocket papillae are typical of hyloid larvae. The buccal pockets are long and very obliquely oriented, with a predominant angle of 30° from the transverse plane. The pockets are definitely perforated, but the slits are obscured from dorsal view by strong forward projections of the mediodorsal portion of the posterior pocket walls. The extensive free velar surface is supported by long, thin spicules that nearly reach the velar margin, which is a relatively smooth broad arch. Marginal projections over the filter cavities are single, faint peaks. The medial portion of the velar margin is the smoothest segment, with only the tiniest median notch. A very narrow band of moderately large and distinctive secretory pits lines the dorsal surface of the velar margin. The pits are absent

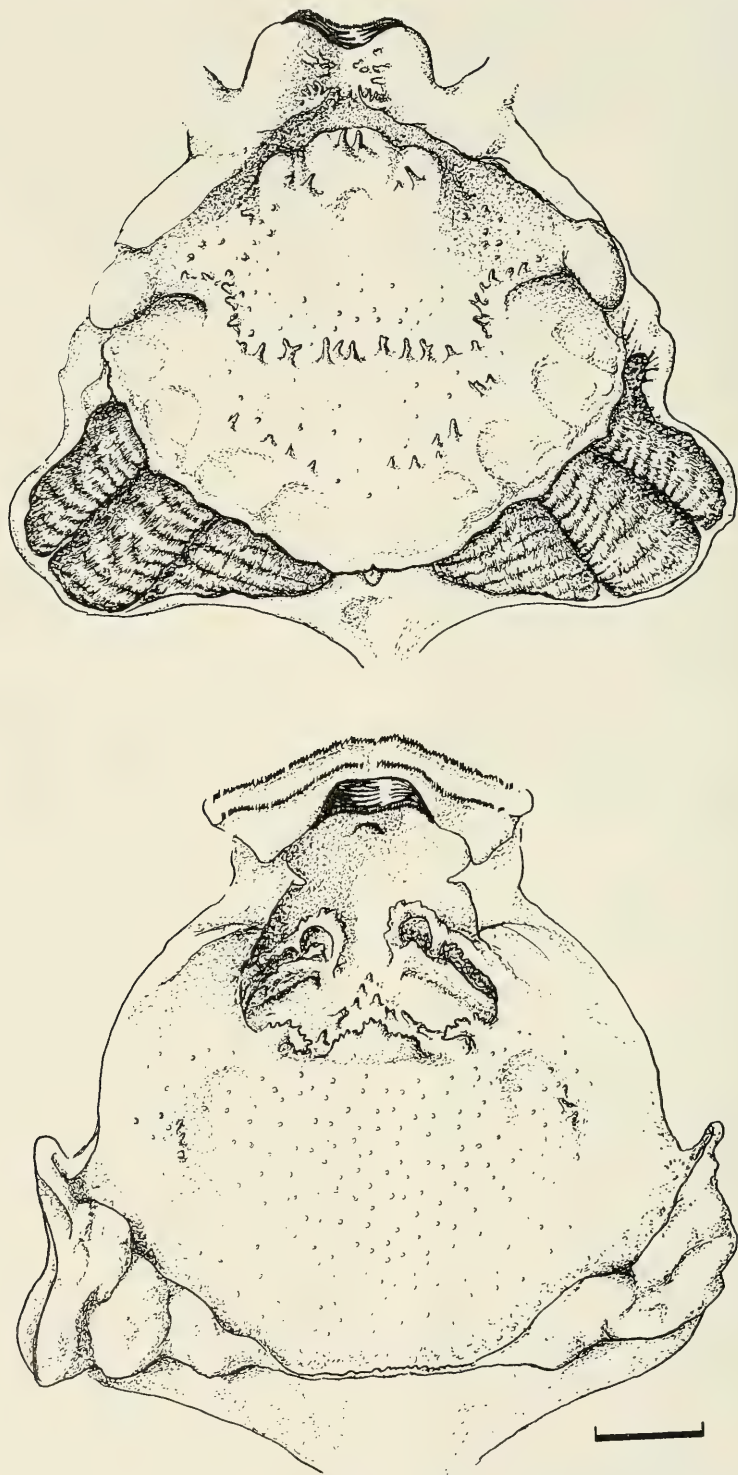


FIG. 21.—Drawings of the floor (above) and roof (below) of the mouth of a *Hyla ruftela* larva.

lateral to the tip of the spicule over cb. 2 and in the immediate neighborhood of the median notch.

Ventral pharynx.—The branchial baskets *in toto*, and the filter cavities in particular, are large, despite the fact that the width to length ratio for the branchial baskets is not unusual. The increased size is reflected in counts of filter rows, *viz.* 9, 11, 11, 9 for cb. 1-4. These are higher than for most hylids examined, the count for cb. 4 significantly so. Ratios of length to height for the filter plates are not great. Thus, although the plates are longer, they are not taller. The filter mesh is dense; filter rows are wide and secondary filter folds are long. There are few partial filter rows. The filter canals are fully canopied. The branchial food traps are long because the velar surface is large. The traps, however, do not cover a great vertical area and are presumably limited by the shallowness of the branchial baskets. Secretory ridges are visible through the velum. These are extremely uniform in spacing and shape and continuous above all the filter cavities on each side. The glottis is 80% blanketed by the ventral velum. The glottal lips are of uneven thickness (thickest posteriorly) but of typical elevation. The esophageal funnel has a slightly narrower dorsal profile than in typical hylid larvae.

Dorsal buccal.—The buccal roof has the same general positioning of major features, such as nares and median ridge, of most hylids; specific regions, however, differ grossly. In the middle of the prenarial arena is a small transverse pustulate row, or low ridge, no wider than the internarial distance. The anterior narial wall makes a full loop into the prenarial arena on each side, forming huge vacuities with high, thick, pustulate walls. Although these pockets are attached to the internal nares, they are *cul de sacs* with smooth round bottoms. These structures may be Jacobson's organs, but they have not been seen in any other hylids. Lateral to these

pockets the anterior narial wall has one to three tiny, pointed prenarial papillae and pustulations. The narial opening is a large elongate oval, oriented a bit more obliquely than in typical hylid larvae. The posterior narial walls are tall with an arched ventral margin. Narial valve projections have pustulate apices that extend forward part way under the unusual prenarial vacuities. There are six to eight postnarial papillae, with additional pustulations; these loosely aligned in a broad, anteriorly directed "V." The papillae are all rather small, subequal, blunt cylinders. The larger are the more posterolateral and tend to have terminal pustulations. The median ridge is more rectangular than triangular. Its free margin is slightly sculptured with faint serrations; a few pustulations occur on the ventral half of the anterior surface. Lateral ridge papillae are shaped like halves of crescents with their peaks pointed medially. Their longer, more anterior margins are strongly serrated. Two or three tiny, pointed papillae are found in the lateral margins of the buccal roof, but they do not define a BRA. Instead, there are 200 or more small pustulations evenly spaced in the middle third of the buccal roof. These thin out laterally. The glandular zone is made up of large, distinctive secretory pits. The zone, overall, is short and of uneven length. The zone is longest laterally and nearly absent on the midline. The dorsal velum is of normal proportions or of slightly greater lateral length than in other hylids examined. It extends across the midline as a low, but movable flap-like ridge.

Dorsal pharynx.—Pressure cushions are present as two large, obliquely oriented bulges on the posterior surface of the dorsal velum on each side. These are more distinctive than those seen in other species of the genus. The lateral cushion is the longer; the medial cushion is the rounder. Medial to the inner cushion on each side is a small roll in the dorsal velum which may be a vestige of



FIG. 22.—Photographs of the floor (above) and roof (below) of the mouth of a *Hyla rufitela* larva.

a third cushion. Behind the pressure cushions are comparatively broad, shallow ciliary grooves.

Diagnostic summary.—*Hyla rufitela* differs from all other tadpoles examined by the development of large *cul de sac* vacuities extending anteriorly from the anterior narial walls.

Hyla dendroscarta Taylor

(Fig. 23)

Material.—MVZ uncatalogued (stage 26, sv. 12.0 mm). Collected from large bromeliad by the road at 1400 m elevation (Highway 150), approximately 5 km W Orizada, Vera Cruz, Mexico; Sept. 16, 1972.

Reference. — Duellman, 1970 (p. 436).

External.—*Hyla dendroscarta* larvae are extremely elongate, with a dorsoventrally flattened body and a sinistral spiracle. The denticle pattern is 3/4.

Ventral buccal.—The buccal cavity is squarish, rather broad anteriorly. The infralabial papillae are simple pads that lack secondary papillae and pustulations. They are of moderate size and just touch on the midline. There are two, typical, lingual papillae. The BFA is well demarcated by two nearly straight rows of papillae that converge posteriorly to form a "V." I counted eight on one side and nine on the other, with an equal number of pustulations arranged along the same general line as the papillae. Some small additional papillae occur lateral to the posterior margin of the arena. All the papillae have sharp apices. The central region of the arena is bare. The prepocket region is bare. Careful manipulation failed to reveal open buccal pockets at 50 \times magnification. The free velar surface is of average length for typical pond larva, but has a relatively dense glandular margin. Individual secretory pits could not be resolved at 125 \times . Supporting spicules appear to be relatively short but the margin appears quite stiff. There are a few minor crenulations and a deep median

notch over the glottis, but no distinctive marginal papillae.

Ventral pharynx.—The branchial baskets are oval, almost round, in dorsal view with a length to width ratio of about 1. They are of average depth, compared to other hylids of similar size. The first and second filter cavities are quite open and fully exposed from above. The third filter cavity, however, is small and largely hidden by the imbrications of the filter plates on the third ceratobranchial. The dorsal margin is straight on the second filter plate, but has a distinctive apex on the third filter plate. I counted: 10 filter rows on cb. 1; 10 on cb. 2; 10 on cb. 3; 7 on cb. 4. The filter rows are particularly dense and thick at the base of the branchial baskets. They are packed such that without subjecting them to extreme manipulation they completely obscure the gill slits in dorsal view. Partial filter rows are short. The density of the filters at the base of the filter rows, is an unusual feature; the filter density overall is slightly less than that of typical pond hylids, largely due to more open filter canals. The ventral surface of the ventral velum is covered by secretory tissue, evidenced by its buffed texture and staining properties. The branchial food traps are relatively short and well organized secretory ridges were not observed. The glottis is well developed particularly for a tadpole of this stage. The glottis lies more than half way under the margin of the ventral velum but is still fully visible in dorsal view because of a large notch above it. The pharyngeal disc is not particularly elevated. A tiny papilla projects up from the front of the glottal lips where they meet on the midline. This is completely hidden in the undistorted specimen by the ventral velum.

Dorsal buccal.—The roof of the mouth shares with the floor a generally squarish shape. The nares and median ridge have a typical position in the mouth for hylid larvae. There is a small

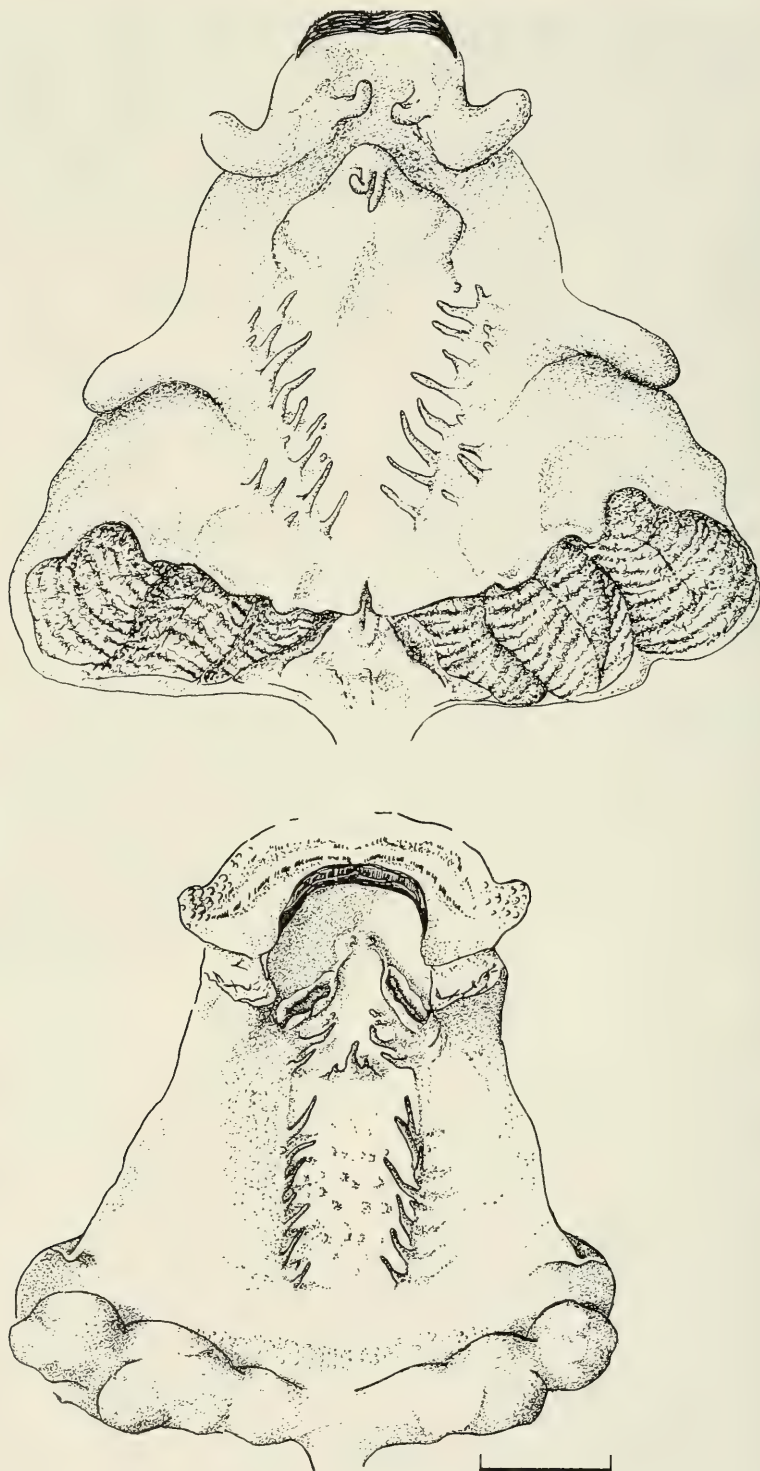


FIG. 23.—Drawings of the floor (above) and roof (below) of the mouth of a *Hyla dendroscarta* larva.

medial swelling in the prenarial arena. In the middle of this swelling are two, short, blunt papillae oriented on a transverse line and adjacent to each other at the midline. The nares are obliquely oriented with a slightly swollen rim surrounding them both anteriorly and posteriorly. A few minor pustulations arise from the lateral portions of the narial wall, but prenarial papillae proper are absent. The narial valves are large free flaps with a distinctive projection arising between the midpoint and the medial margin of the posterior wall. The postnarial arena is triangularly shaped and is defined anteriorly by a short row of papillae, two on one side and three on the other, plus a relatively small median ridge posteriorly. The short median ridge has three distinctive projections with the single medial one most distinctive. Lateral to the median ridge are two attenuate lateral ridge papillae, one of which has a secondary pustulation near its base. These lateral ridge papillae are in line with two rows of buccal roof papillae that extend backward in almost parallel lines. Pustulations are lacking in the postnarial arena but are quite evident in the BRA. The BRA is a tall trapezoid with the median ridge and the lateral ridge papillae forming the wider base. Seven tall papillae, all lacking secondary pustulations, form the BRA papillate rows on each side. Papillae and pustulations are lacking elsewhere on the buccal roof. The glandular zone is short with a relatively uniform length from the lateral margin of the roof of the mouth to the midline.

Dorsal pharynx.—The dorsal velum is also short with two, distinctive, round pressure cushions of subequal size. The dorsal velum is absent on the midline. The esophageal funnel has a narrow profile. The ciliary groove is barely visible laterally but it is a distinct, open trough as it leads into the esophagus.

Diagnostic summary.—The varying density of gill filters—very dense ventrally and much less dense dorsally—

readily characterizes this larvae. This feature, however, may simply reflect the early ontogenetic stage of this specimen (*H. dendroscarta* larvae are rare in collections and this was the largest specimen available for study. The specimen was 40% longer than a free-living, feeding, stage 25 individual also examined). Several less questionable, but also less obvious features collectively distinguish this larvae from others examined. These include: simple, blunt infralabial papillae in association with tall, attenuate BFA, BRA and lingual papillae; absence of obvious secretory pits or ridges in branchial food traps, presence of papilla at anterior edge of glottis; thickened rim around nares.

Hyla phlebodes Stejneger
(Fig. 24)

Material.—KU 68405 (stage 31, sv. 7.3 mm). Collected in forest pool at 100 m elevation, Puerto Viejo, Heredia, Costa Rica; July 15, 1961.

Reference.—Duellman, 1970 (p. 222).

External.—*Hyla phlebodes* (like other members of the *Hyla microcephala* species group) is characterized by a tail that terminates in a long pointed filament, tiny recessed beaks, and the absence of denticles and oral disc papillae. The spiracle is sinistral.

Ventral buccal.—The trend toward reduction of oral structures seen externally is continued internally; this reduction is greater in *H. phlebodes* than in other *Hyla* larvae examined. The floor of the mouth is disproportionately elongate anterior to the buccal pockets. Because of the tiny beaks the mouth comes to an acute anterior termination. Single, relatively huge, infralabial papillae on each side overlap one another at the midline. These are roundish, slightly antero-posteriorly compressed structures, which lack any secondary projections. Each is larger than the oral orifice. There are no other papillae anywhere inside the mouth. The only surface features arising from the buccal floor

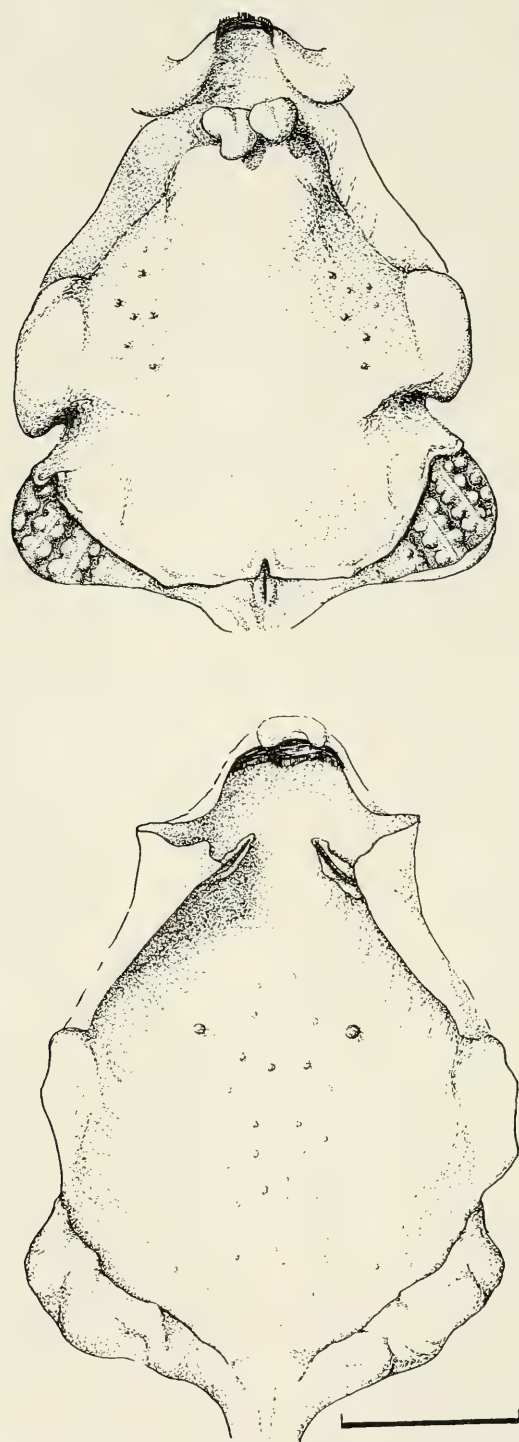


FIG. 24.—Drawings of the floor (above) and roof (below) of the mouth of a *Hyla phlebodes* larva.

are five or six tiny pustulations above the lateral portion of the ceratohyal on each side. The buccal pockets are tiny, shallow and unperforated. They extend back from the midline at a great angle. The free velar surface is very short and unsupported by spicules. The trailing edge is a smooth curve without any posteriorly directed projections although a large, deep, median notch is present. Secretory pits could not be resolved on the velar margin and are probably absent.

Ventral pharynx.—The branchial baskets are reduced in all planes. Filter plates are practically absent. Knobs on the gill bars, vestiges of filter rows, line the gill slits. These "filter rows" number 4, 5, 5, 3 for ceratobranchials 1-4 respectively. Filter folds are absent. There is little space left for branchial food traps in the shallow pharynx, and they may be absent. Secretory ridges, if present, would have to be restricted to the ventral surface of the velum, but none could be resolved on that surface. A large glottal slit fills the median notch of the velum. The slit sits on well-developed, elevated lips and is fully exposed when viewed from above. There is a large, unelevated laryngeal disc. Behind this extends a broad esophageal funnel.

Dorsal buccal.—The buccal roof, like the buccal floor, is elongate. The nares are far anterior and the prenarial arena is proportionally small. Surface structures are absent in the prenarial arena. The internal nares are small slits oriented at an angle 35° from the transverse plane. The narial walls are not tall and lack any sculpturing such as prenarial papillae or narial valve projections. Not quite halfway back on the buccal roof are two single pustulations, one each aligned directly behind the lateral margins of the nares. With intense staining some faint pustulations may be seen on the middle posterior portion of the roof. The buccal roof is otherwise devoid of any ridges, pustulations, papillae, etc.

A discrete anterior margin for the secretory zone could not be resolved, although tiny secretory pits are present posteriorly in the esophageal funnel. Remnants of a dorsal velum are present as two tiny, asymmetric, anteriorly directed flaps. These flaps are completely absent both in front of the large esophageal funnel and laterally; in total they traverse only a quarter of the mouth.

Dorsal pharynx.—The two small flaps identified as remnants of the dorsal velum are far posterior and a dorsal pharynx is essentially absent. Pressure cushions are not present and the ciliary groove is a tiny crease behind the vestigial dorsal velum.

Diagnostic summary.—Some material of *Hyla microcephala* has been available for study; in that no major differences were found between *H. microcephala* and *Hyla phlebodes*, the following diagnosis can stand as a diagnosis for the *H. microcephala* species group as a whole. These larvae can be distinguished from all other tadpoles examined by the unique knob-like vestiges of the filter rows on the diminutive ceratobranchials. In addition, *H. phlebodes* has the most massive, and unusually shaped, ceratohyals (and associated musculature) of any *Hyla* examined. The following selected features in combination further diagnose this species: large, medially, overlapping infralabial papillae; buccal papillae absent; glottis large; branchial baskets very small and filter row remnants few in number; secretory ridges absent; esophageal funnel large.

Hyla mixe Duellman

(Fig. 25)

Material.—KU 104183 (stage 28, sv. 11.8 mm). Collected attached to small stones in gravel-bottom pools in cascading small stream on N slope of the Sierra de Juarez, 4.2 km S of Compamento Vista Hermosa, Oaxaca, Mexico; February 16, 1966.

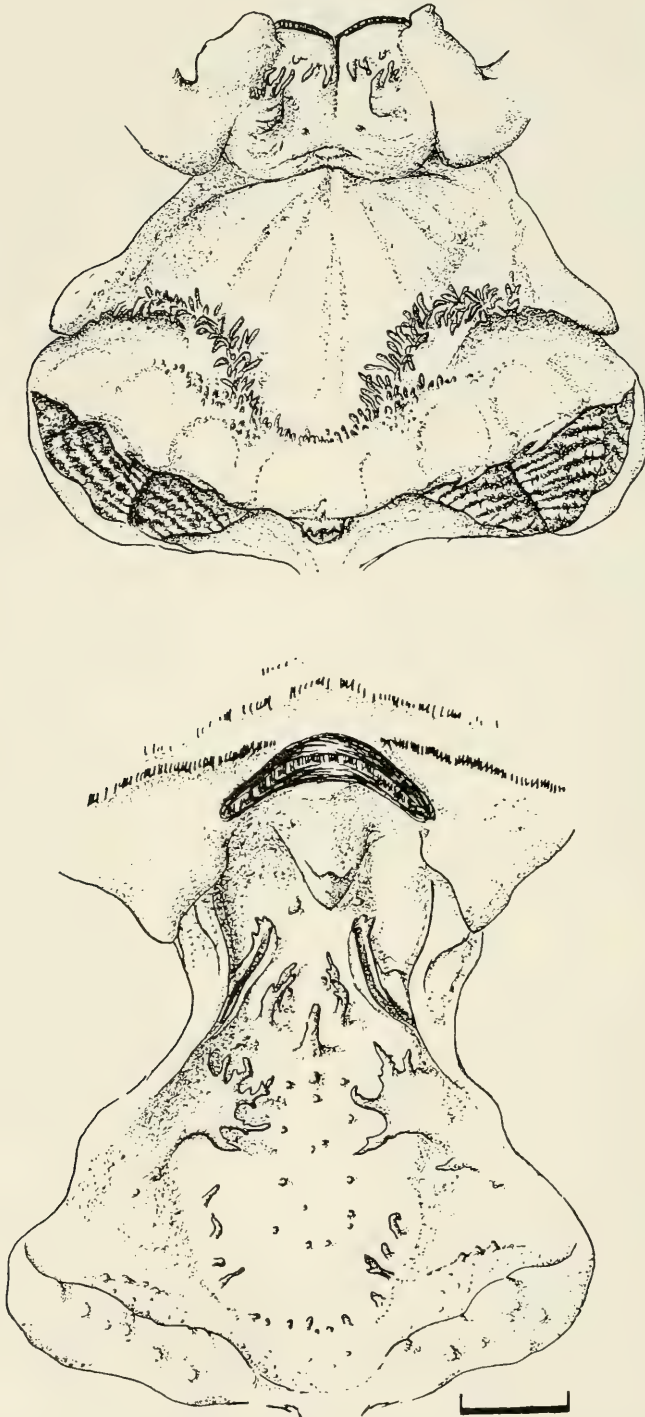


FIG. 25.—Drawings of the floor (above) and roof (below) of the mouth of a *Hyla mixe* larva.

Reference.—Duellman 1970 (p. 426-427).

External.—Tadpoles of this genus have a relatively huge, ventral, oral disc with a 7/10 to 7/11 denticle pattern. The spiracle is sinistral.

Ventral buccal.—The width to length ratio of the whole oral cavity reveals a relatively short oral cavity in this species. These tadpoles have the most extreme proliferation of internal oral papillae seen in any *Hyla*. Five small posteriorly directed papillae are present at the anterior limit of the infralabial region. These are evenly spaced immediately behind the keratinized beak. Two, major, fringed flaps are behind this row and quite similar in shape and position to typical hand-like infralabial papillae. These later papillae are wide, and their secondary marginal papillae (four per side) are long and attenuated. Fine tertiary divisions of the marginal papillae are present on both sides. Two pustulations are present adjacent to the midline between the major pair of infralabial papillae. No other symmetrical projections neighbor the midline in the immediate region behind these pustulations, so they may be the homologues of the lingual papillae despite their relatively anterior position and small size. The buccal floor arena is sharply demarcated posteriorly and laterally by a continuous fringe of 70 small to medium-sized, pointed papillae. The fringe begins far laterally in front of the buccal pockets, curves mesad around the end of the pockets, and continues obliquely to a point on the midline just anterior to where the free velar surface begins. The BFA papillae and prepocket papillae series are thus connected. This line of papillae is occasionally two papillae wide along its length. The papillae in the anterolateral and posteromedial portions of the BFA are the shortest. The tallest papillae are immediately medial to the buccal pockets. A very few of the larger papillae exhibit bifurcations near their bases. Many of the

larger papillae have bumps or pustulations about halfway from their base. The papillae are virtually all curved; those in the typical BFA position are curved anteromedially; those in the prepocket position arch directly posterior over the buccal pockets. Anterior to the fringe the buccal floor is void of pustulations or projections. Behind the fringe are secondary transverse rows of very small, anteriorly curved papillae. These rows are made up of five papillae on one side and four on the other. They are restricted to the areas between the base of the spicules of cb. 2 and cb. 3 on the most posterior part of the non-velar buccal floor. The buccal pockets are slender and transversely elongate. They are deep and each is occluded by a large, anteriorly directed fold arising from the posterior dorsal surface of the pocket on each side. The overhanging papillae from the prepocket portion of the papillae wall on the buccal floor further obscures the entrance to the buccal pockets. It is doubtful that the pockets are perforated in this species. Although the ratio of the length of the mouth to the maximum length of the velum is within the range for more typical hylids; the total velar area may actually be a bit larger. The supporting spicules are relatively heavy and long. They reach the posterior margin of the velum, causing protuberances in the velar margin visible from above. Four undulating peaks on the velar margin are distinctly leptokurtic; they point posteromedially rather than posteriorly. Two auxiliary peaks neighbor the median notch. A few small secretory pits were seen on the dorsal surface of the posterior edge of the velum, but the overall density or anterior extent of the secretory pits could not be assessed.

Ventral pharynx.—The branchial baskets are relatively short, and this may account for the appearance of shortening in the whole oral cavity. The most extensive reduction is in the fourth ceratobranchial. Compared to other mem-

bers of the genus, the branchial baskets are shaped as if they were pushed outward along their posteromedial margin. The third filter cavity is a slim, deep pocket concealed by the recumbent dorsal margin of the filter plates on cb. 3. Because the branchial baskets are short while the velum is not, the filter cavities are blanketed more fully by the velum than in most species examined. Less than 10% of filter cavity 3 lies behind the trailing edge of the ventral velum. In terms of relative height of the filter plates and numbers of filter rows (i.e., cb. 1 = 10, cb. 2 = 10-12, cb. 3 = 9-10, cb. 4 = 4-5), *Hyla mixe* is not significantly different from more typical hylid larvae. The filter mesh is less dense. Secondary and finer filter folds are thin and the space between neighboring filter rows is large. Thus, the filter canals may be slightly more open in *H. mixe* than in other congeners. The large, stiff spicules made exploration of the ventral velar surface particularly difficult and I could not resolve secretory ridges anywhere under the velum. However, in this specimen broad bands of light, flocculent food matter were adhering to the ventral surface of the velum parallel to the posterior velar margin, suggesting the presence of some organized secretory tissue in this region. The glottis is open and slightly elevated but glottal lips are absent and the laryngeal disc is not visible; this may in part reflect the early developmental stage of this specimen. The glottis is more than 80% hidden from dorsal view by the edge of the velum. Behind the glottis is a moderately broad esophageal funnel.

Dorsal buccal.—A massive soft, fleshy cone extends down from the prenarial arena into the medial space between the infralabial papillae. The base of the structure is oval in shape, about half as long as wide, and is 50% wider than the internarial distance. The height of the cone is equal to its width. As the cone descends it gently curls anteriorly. A half dozen pustulations cover the sides

of the cone near its pointed tip. Directly in front of the internal nares are single, small, thin papillae, one on each side. No other structures are present in the prenarial arena. The internal nares are $3\frac{1}{2}$ times wider than long (length measured along longer axis), significantly longer than in more typical hylid larvae. The angle made by the long axis of the internal nares from the transverse plane (45°) is very large. The anterior narial walls are characterized by a few knobby pustulations and a single tiny papilla on each side very near the anteromedial corners on each side. The posterior wall is not very tall and completely lacks a narial valve projection. Each side of the postnarial arena is bound by a straight row of three attenuate postnarial papillae. These rows are oriented nearly parallel to the sagittal plane, but with their most anterior papillae slightly closer than their posterior papillae. The three papillae on each side increase in size from front to back. The largest one is as tall as the conical protuberance in the prenarial arena. The two other posterior papillae in each row arch slightly medially and have secondary pustulations on their anterior margins. In the position of the median ridge is a single, tall, extremely attenuate papilla which curves slightly anteriorly and has a rugose anterior surface. It is subequal to the tallest postnarial papillae. There are no pustulations within the postnarial arena. Two projections are evenly spaced directly behind the median papilla on the midline. The anterior one is a plain, small papilla; the posterior one is but a pustulation. The lateral ridge papillae are developed into relatively huge, longitudinally oriented, papillate flaps. The flaps are as tall as long and point medially. They are displaced slightly posterior in relation to the median (ridge) papilla. Distinct attenuate marginal papillae, four on one flap and five on the other, account for more than half of the maximum height of these projections. The marginal "papillae" have pustulate

sides in addition to one or two minor basal bifurcations. The median (ridge) papilla and the flap-like ridge papillae outline the anterior end of a large, nearly rectangular, buccal roof arena. The posterior portion of this BRA is defined by lateral rows of five simple, thin papillae. The first four in each row are in a continuous line running back from the flap-like lateral ridge papillae. The last and smallest papilla in each row is displaced medially. The tallest papillae in the BRA series are half the height of the lateral ridge papillae. Some half dozen faint pustulations are scattered in the anterior end of the BRA. Lateral to the BRA and two-thirds of the distance back on the buccal roof are single, small papillae, one per side. The only other features on the buccal roof are some pustulations directly behind these lateral roof papillae. These pustulations contact the anterior edge of the glandular zone. The glandular zone has a very uniform, buff texture. It was virtually impossible to resolve the individual miniscule secretory pits of the glandular zone even at 75 \times . The anterior margin of the secretory zone is arched posteriorly, so that the zone has a 50% greater length laterally than on the midline. The dorsal velum is strongly coiled, but did not appear to be particularly long in this specimen (some of the dorsal velum was destroyed in dissection). If the velum is continuous across the midline, it is not exceptionally tall in that region.

Dorsal pharynx.—A single, shallow, mediolaterally elongated pressure cushion could be resolved on one side but was removed from the specimen along with portions of the dorsal velum in order to gain access to the filter cavities during the study of ventral features. Details of the ciliary groove could not be determined.

Diagnostic summary.—*Hyla mixe* tadpoles are unique among the tadpoles examined in having the papillae of the buccal floor arena so numerous and close to each other that a continuous fringe is

formed. The larva are also distinguished by having: reduced third filter cavities; a massive cone-like projection of the prenarial arena; a median ridge reduced to a papillae; extremely large lateral ridge papillae.

Hyla ebraccata Cope

(Fig. 26)

Material.—KU 104130 (stage 35, sv. 10.8 mm). Collected amidst emergent weedy, vegetation in shallow pond in clearing at edge of forest, at 100 meters elevation, Puerto Viejo, Heredia, Costa Rica; June 21, 1966.

Reference.—Duellman, 1970 (p. 230-232).

External. — *Hyla ebraccata* larvae have a long, pointed filamentous tail. They have a small, anteriorly directed mouth without denticle rows and a highly reduced oral disc. The eyes are far lateral; the spiracle is sinistral.

Ventral buccal.—These larvae are characterized by a series of reductions in the oral cavity from what may be considered the typical anuran condition. Single anterior to posterior compressed infralabial papillae are present on both sides. These small, flap-like papillae are approximately twice as wide as tall and have a slightly rugose dorsal margin. On the midline are a pair of small papillae which may be homologues of the lingual papillae. Their far forward position, on the infralabial cartilage directly between the infralabial papillae, speaks against homologizing these projections with the lingual papillae; on the other hand, there are no other papillae directly behind them and the anlage of the tongue is absent. Five or six very fine, simple papillae are dispersed laterally about the buccal floor and in front of the buccal pockets. A buccal floor arena *per se* is absent. Pustulations present on the buccal floor are scattered largely in front of the buccal pockets and are about as numerous as the buccal floor papillae. The buccal pockets are shallow and clearly not perforated. The

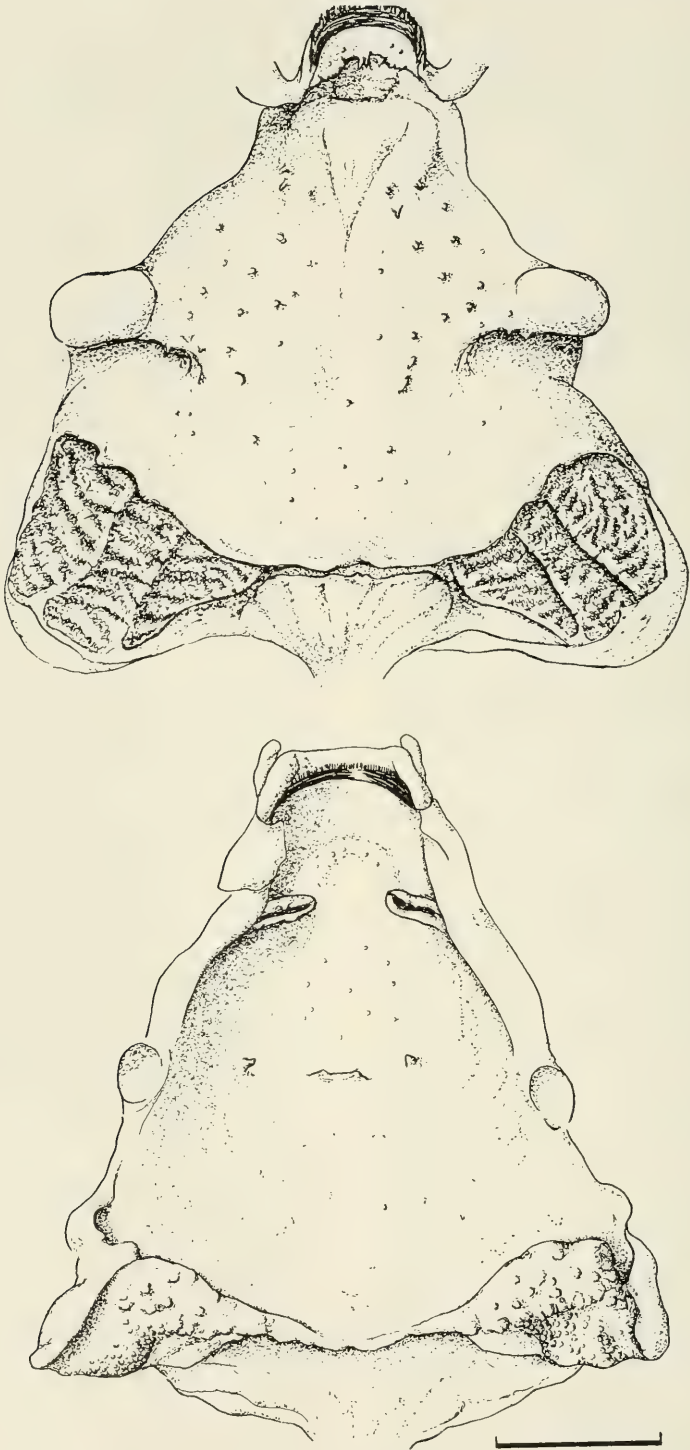


FIG. 26.—Drawings of the floor (above) and roof (below) of the mouth of a *Hyla ebraccata* larva.

trailing edge of the ventral velum is a rather smooth semicircle. The undulations in the edge normally present above each filter cavity in other hylid larvae are reduced greatly in amplitude. The lateral peaks over filter cavity 1 are more distinct than those over filter cavity 3. The medial portion of the velar margin has a weak notch but is, otherwise, free of any abrupt contouring. Tiny secretory pits are on the dorsal velar margin. These occur quite far forward and cover much, if not all, of the free dorsal velar surface. The pits are densest near the midline. The free velar surface is comparatively short considering that the spicules are quite long. This makes the edge rather stiff and immobile medially. The free velar surface also tends to be thick; secretory ridges cannot be seen without turning the edge over.

Ventral pharynx.—The branchial baskets are about as long and wide as in typical members of the genus, but not nearly as deep. The filter plates are so short, and imbricated to such an extent, that filter tissue on cb. 2 and 3 is virtually restricted to the lateral faces. The filter plates of the first three ceratobranchials are four to five times as long as high. Those of the fourth ceratobranchial are about twice as long as high. The number of full filter rows on the filter plates are: cb. 1 = 8, cb. 2 = 8-9, cb. 3 = 11, cb. 4 = 8-9. Except for the high number of filter rows on cb. 4, these are well within the range for more typical hylid larvae. There are no partial filter rows. The filter mesh is very loose and, although secondary filter folds are numerous, they are quite thin and tertiary folds are lacking. Neighboring filter rows on each filter plate do not abut, consequently, filter canals are open channels along their whole length. Well defined branchial food traps are associated only with the third filter cavity; all secretory ridges are concentrated laterally and restricted almost completely to the horizontal surface of the velum. Where secretory ridges appear, they are

moderately wide and not dense. The trough between the secretory ridges is shallow. As viewed from above about half of the glottis is under the velum. The laryngeal disc is transversely elongated. The posterior margin of the disc is turned up so that the glottal slit is oriented more vertically than horizontally. Glottal lips are well developed. The esophageal funnel is broad and the lumen of the esophagus extremely large. The funnel is tightly juxtaposed to the laryngeal disc and by its mere size seems responsible for the distortion in the laryngeal disc.

Dorsal buccal.—The prenarial arena is short. A single, relatively large bulge, which is convex anteriorly, arises in this arena and takes up most of its area. There are between one and two dozen tiny pustulations in the prenarial arena, mostly on the margins of the "bulge." The internal nares are small; narial walls are not tall. Prenarial papillae are absent from the anterior walls, although the walls' margins are slightly rugose. The narial valves are two to three times as wide as tall and lack narial valve projections. Both postnarial and buccal roof arenas are absent. A short, transverse crease halfway back on the buccal roof may be a remnant of the median ridge. It is not particularly wide, nor straight, and is relatively farther posterior than the median ridge in most Orton type 4 tadpoles. In front of this crease are a dozen or so very tiny, pointed pustulations. These are absent in the back half of the buccal roof. The only papillae on the buccal roof are two, lateral to the median (ridge) crease and displaced slightly forward. These papillae are small, simple and may be considered either lateral ridge or buccal roof papillae, depending on the faith one has in the homology of the "crease" with the median ridge. The tiny secretory pits, comprising the glandular zone, are sufficiently difficult to resolve that the anterior limits of the zone cannot be determined. Laterally, the dorsal velum

is short; however, the velum is continuous across the midline. Whereas the lateral portions of the dorsal velum project anteriorly, the velum twists sharply to project directly caudad on the midline. This middle portion of the velum is half as long as the velum at its widest lateral point.

Dorsal pharynx.—Both medial and lateral pressure cushions are fused into a single, relatively large but shallow, roundish pad. Consistent with the large esophageal funnel, the ciliary groove is wide and not very deeply entrenched.

Diagnostic summary.—See *Hyla sarayacuensis* (p. 72).

Hyla sarayacuensis Shreve
(Fig. 27)

Material.—KU 121413 (stage 34, sv. 11.1 mm). Collected in grass marsh at 1260 meter elevation, Rio Negro, Tungurahua, Ecuador; July 25, 1968.

Reference.—None.

External.—The larvae of *Hyla sarayacuensis* have not been described in detail. It is sufficient to say that *H. sarayacuensis* tadpoles possess the assortment of larval features characteristic of the *Hyla leucophyllata* group: a tiny inset terminal mouth, absence of a papillate labial disc and denticle rows, xiphiceral tail filament with tall equal or subequal dorsal and ventral fins. The spiracle is sinistral. Compared to *H. ebraccata*, *H. sarayacuensis* tadpoles have a relatively tall tail.

Ventral buccal.—The interior of the mouth of *H. sarayacuensis* is so similar to *H. ebraccata* that all features which unify the two species and contrast them with more typical *Hyla* larvae are not repeated. Instead, emphasis is placed on the few differences between *H. sarayacuensis* and *H. ebraccata*. A single anterior to posterior compressed infralabial papilla is present on each side in *H. sarayacuensis*. These have blunt dorsal margins and are smaller and about half as wide as the infralabial papillae in *H. ebraccata*. Medial papillae of any

sort, such as those suggested as possible lingual papillae in *H. ebraccata*, are absent. The tiny secretory pits on the dorsal edge of the ventral velum are just as dense in *H. ebraccata*, but thin out anteriorly and may not cover the whole free velar surface.

Ventral pharynx.—*H. sarayacuensis* exhibits some slight further reduction in the pharyngeal region compared with *H. ebraccata*. Counts for filter rows on the filter plates run: cb. 1 = 6, cb. 2 = 6-7, cb. 3 = 8, cb. 4 = 8. The values for the first three ceratobranchials can be considered low; those for cb. 2 significantly so. Again, the number of filter rows on cb. 4 is significantly above the average for more typical larvae of the genus. Only with the greatest difficulty and repetitive staining could secretory ridges be resolved under the ventral velum. Branchial food traps are not well demarcated. The greatest concentration of secretory ridges seems to be lateral and anterior and even here the topography is quite faint.

Dorsal buccal.—As in *H. ebraccata*, in the prenarial arena a faint, anteriorly convex bulge is seen, but pustulations are absent. Small prenarial papillae are present, three on one side and one on the other. These projections arise from the medial half of the anterior narial walls. Other pustulations or rugosities are absent from the narial walls. The two lateral roof papillae, seen in *H. ebraccata*, are present in *H. sarayacuensis*. They are slightly behind the median papilla and half the distance laterally. In this specimen the anterior margins of the secretory zone could be resolved. The zone is of uniform length and has a smooth semicircular anterior margin. The ratio of the length of the buccal roof to the length of the glandular zone was 4:1, which means that the zone is unusually long. The dorsal velum is similar to *H. ebraccata* but has slightly shorter median and lateral lengths.

Dorsal pharynx.—Details of the dor-

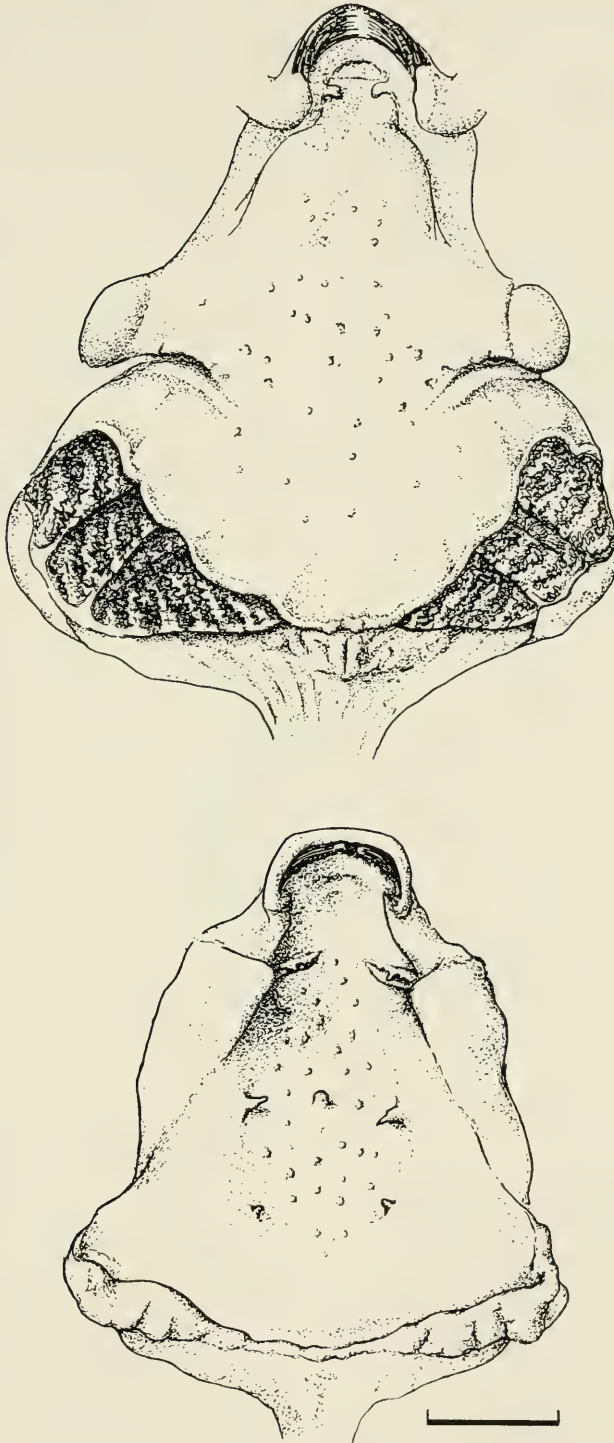


FIG. 27.—Drawings of the floor (above) and roof (below) of the mouth of a *Hyla sarayacuensis* larva.

sal pharynx region could not be determined because of damage during dissection.

Diagnostic summary.—*Hyla ebraccata* and *Hyla sarayacuensis* as representatives of the *Hyla leucophyllata* species group are characterized by the following oral features: medially elongate prepocket buccal surface; reduction of the oral papillation and projections that define arenas; reduced marginal projections of ventral velum; proportionally large third filter cavity with comparatively high number of filter rows in cb. 4; less dense filter mesh than typical (2/3 denticle patterns) hylid tadpoles; reduction of area of secretory ridges in the posteromedial portion of the branchial food traps; secretory pits covering extensive areas of dorsal surface of ventral velum and posterior buccal roof; large esophageal funnel. Both *Hyla ebraccata* and *Hyla sarayacuensis* tadpoles are definable by the combination of characters given above; the differences between these two species are minor and given in the descriptions.

Ptychohyla schmidtorum chamulae

Duellman

(Figs. 28, 29)

Material.—KU 75409 (stage 35, sv. 12.7 mm). Collected attached to stones in pools in montane stream at 1600 meters elevation, 17.6 km NW of Pueblo Nuevo Solistahuacan, Chiapas, Mexico; June 14, 1963.

Reference.—Duellman, 1970 (p. 529-532).

External.—A slightly elongate tadpole, with a 3/3 denticle pattern. The circumference of the oral disc is expanded into a denticle-free funnel of modest size. The spiracle is sinistral.

Ventral buccal.—The buccal floor is comparatively short and broad. The most anterior features in the mouth are eight medium sized, attenuate papillae, four per side. These line the base of the keratinized beak and arch forward, pointing out of the oral orifice. A bit

more posterolateral on each side are single, large fleshy infralabial papillae. These are slightly compressed and bear faint, terminal pustulations and pointed apices. Dorsolateral to these papillae, over Meckel's cartilage, are soft palps or cushion-like bulges of the buccal lining. These are oval and obliquely oriented. The lingual papillae are exceptionally long and thin, and arch forward. The tongue anlage is narrow and extending obliquely back from its base are two wide but low elevations of the buccal surface. These curve slightly toward the medial margins of the buccal pockets before fading into the buccal floor. The BFA papillae are arranged in a "U" which is open anteriorly. The top of the "U" flares laterally such that the BFA papillae are in a continuous row with the prepocket papillae. These papillae are all attenuate, of small to medium size, with curved pointed tips. I counted 18 on one side and 20 on the other. Two or three of these on each side can be considered prepocket papillae. Only three BFA papillae were bifurcated. The center of the arena is devoid of pustulations. The only pustulations present on the buccal floor are at the posterior margin of the BFA and anterolateral above the body of the ceratohyals. Two or three medially directed papillae are among these anterolateral patches of pustulations. The buccal pockets are wide in *P. schmidtorum*; they are also clearly perforated in this species. *P. schmidtorum* has a relatively large free velar surface supported by 4 pairs of long spicules, the more medial of which fully reach the velar margin. The posterior edge of the velum has moderately acute peaks associated with each filter cavity. The peaks of the third filter cavity are displaced medially and are the largest. In addition to these undulations the velar margin is slightly arched around the tips of the spicules. The middle portion of the velum is strongly emarginated, with four or five papilla-like projections (preserved fold-

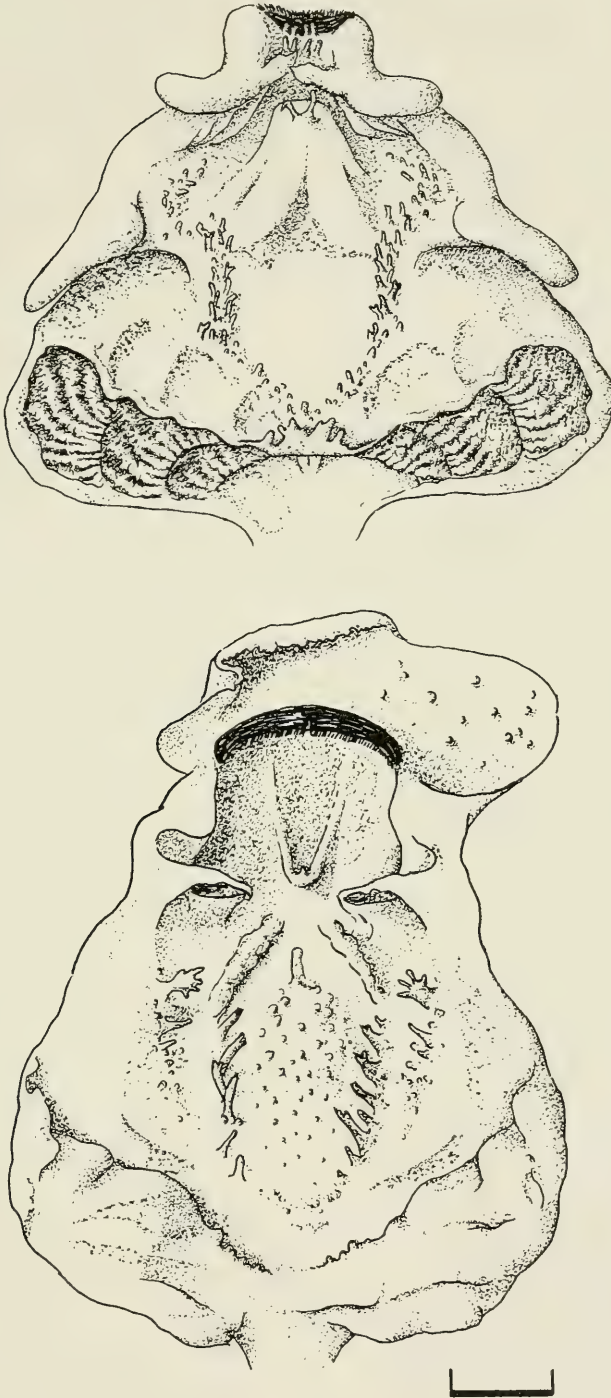


FIG. 28.—Drawings of the floor (above) and roof (below) of the mouth of a *Ptychohyla schmidtorum* larva.

ed up and forward in this specimen). Individual secretory pits could not be resolved on this surface, although the apices of the trailing velar projections tended to have a buffed texture.

Ventral pharynx.—The branchial baskets of *P. schmidtorum* are of average size for a hyloid, but have the appearance of being displaced laterally along their posteromedial border. The baskets are relatively shallow, yet the filter plates are imbricated to an extreme and, consequently, are still quite tall. Ratios for maximum height to maximum length show the filter plates of *P. schmidtorum* to be as tall or taller than typical hyloid tadpoles. Numbers of filter rows on each plate fall well within the normal hyloid range; the filter mesh, however, is not dense. The filter rows are low, narrow creases with short secondary branches. Higher degree folds are rare and, when present, short. They occur predominately along the ventral margin, where the filter rows are their widest. The filter canals are wide, open channels as wide or wider than the filter rows. Secretory ridges are visible through the dorsal surface of the velum; their size and proportions are typical for a hyloid tadpole. The branchial food traps are not unusual. The glottis would not be visible in dorsal view, if the mid-portion of the velum had been preserved in the normal position. The glottis has a small and rather inconspicuous laryngeal disc. The esophageal funnel is not large but has a broad profile in dorsal view.

Dorsal buccal.—Anteriorly the roof of the mouth is slightly expanded, otherwise gross dorsal proportions are typical for a hyloid. There is a central trough that runs the length of the prenarial arena. It is surrounded posteriorly by a narrow V-shaped ridge (open anteriorly) that increases progressively in height toward the internal nares. The ridge terminates posteriorly in a single projection. Other papillae and pustulations in the prenarial arena are absent. The internarial distance is great. The

nares have a nearly transverse orientation and are laterally elongate. Their anterior walls are thin and low; they lack any pustulations or prenarial papillae. Their posterior walls are long and low and narial valve projections are faint or not present. *P. schmidtorum* lacks a well defined postnarial arena. In the position of the median ridge is a single, stiff, tall papilla. Lateral to it are obliquely oriented (anteromedial to posterodorsal) ridges on each side. These ridges have thick, wide bases and curved, bumpy ventral margins. They are tallest and thickest anteriorly, abruptly descending from the buccal roof at a position where one would expect to find the most anterior postnarial papillae in other species. They continue back an equal distance behind the median (ridge) papilla and appear to be homologues of the postnarial papillae. Continuing posteriorly from the end of these oblique ridges are BRA papillae in two lines that converge slightly toward the midline; seven and eight to a side. The first and last papillae in the rows are diminutive; others are moderately large, and the five largest (three on one side, two on the other) have terminal bifurcations. The most posterior BRA papillae are displaced slightly toward the middle, reinforcing the image of a circumscribed "arena." Within the middle of the BRA are approximately 50 pustulations, the ten largest concentrated anteriorly near the base of the median (ridge) papilla. Directly lateral to the end of the oblique ridges are two moderately large, laterally compressed papillae, one per side. Both of these have terminal bifurcations. They also are possible homologues of the lateral ridge papillae. Directly behind these, lateral to the BRA and in a line with the middle of the arena, are tight clusters of small pustulations, including one or two simple, small papillae. Still further posterior, lateral to the end of the BRA, are two small, transversely oriented knolls. The glandular zone is very short



FIG. 29.—Photographs of the floor (above) and roof (below) of the mouth of a *Ptychohyala schmidtorum* larva.

and of uneven thickness. It is nearly absent on the midline but wider laterally. Secretory pits are similar in size and density to many other hyliids examined but are not especially conspicuous, presumably because of differences in preservation. The dorsal velum is slightly shortened; it is completely absent on the midline. The free velar margin is moderately crenulate, particularly medially.

Dorsal pharynx.—Pressure cushions are absent in *P. schmidtorum*. The ciliary groove is very broad and shallow.

Diagnostic summary.—Tadpoles of the genus *Ptychohyla* can be distinguished from larvae of the other hyliids examined by a combination of the following characters: attenuate lingual papillae; buccal floor and roof arenas elongate; median projections of the posterior velar margin elongate; third filter cavity truncated; filter mesh of low density; median ridge attenuate.

Ptychohyla schmidtorum was the only funnel-mouthed hyliid larva I examined. In its oral cavity, the larvae exhibits the assorted modification associated with the funnel-mouthed condition; principally, the fusion of papillae series into ridges and the posteriorly directed V-shaped depression of the pre-narial arena.

Ptychohyla leonhardschultzei (Ahl)
(Figs. 30, 31)

Material.—KU 139924 (stage 26, sv. 14.4 mm). Collected on bottom of riffles in streams at 720 m elevation, 18.1 km N of San Pedro Mixtepec, Oaxaca, Mexico; March 20, 1970.

Reference. — Duellman, 1970 (p. 543).

External.—The body is slightly elongate. The denticle formula is 4/6. The oral disc is relatively large, but does not have the expanded, denticle-free margin seen in *P. schmidtorum*.

Ventral buccal.—The floor of the mouth in *P. leonhardschultzei* is relatively short; it has a squarish shape. In

a transverse row at the base of the keratinized beaks are two pairs of small, jagged papillae. The smaller of the pairs is more lateral. Several subpapillate pustulations are still more lateral. Behind these pustulations on each side is a major infralabial papilla, shaped like a cupped hand with long, pointed "fingers" projecting forward. The fingers, four and five per side, have scattered, pointed pustulations on their margins. The two lingual papillae are very attenuate, as are most other oral papillae. The BRA is an elongate oval. The arena is surrounded by 86 moderately tall, thin, pointed papillae in this specimen. These papillae are strongly curved so as to point medially. Clusters of papillae near the lateral ends of the buccal pockets are fused at their base to form multi-papillate structures which look like miniature deer antlers, one per side. These have six "points" on one side and eight on the other. Only two other papillae on the buccal floor show any sign of bifurcation. There are three and four small, conical prepocket papillae on opposite sides. Between the anterior end of the BFA papilla series and the prepocket papillae are twelve to twenty papillae of the same shape and size as those in the BFA series. These fully cover the surfaces above the body of the ceratohyals. Papillae from the BFA series also extend laterally behind the buccal pockets to cover a small region of the buccal floor anterior to the second filter cavity. There are some 60 or so very tiny pustulations dispersed within the buccal arena. The buccal pockets are long, shallow, and perhaps a bit more transversely oriented than in typical hyliid larvae. They are conspicuously perforated. The free velar surface is large. It is supported by stiff spicules; the more medial pairs reach the velar margin. Single, symmetrical, leptokurtic projections of the velar margin are aligned over filter cavities 1 and 2; the more medial of these projections point posteromedially. Eight other distinct

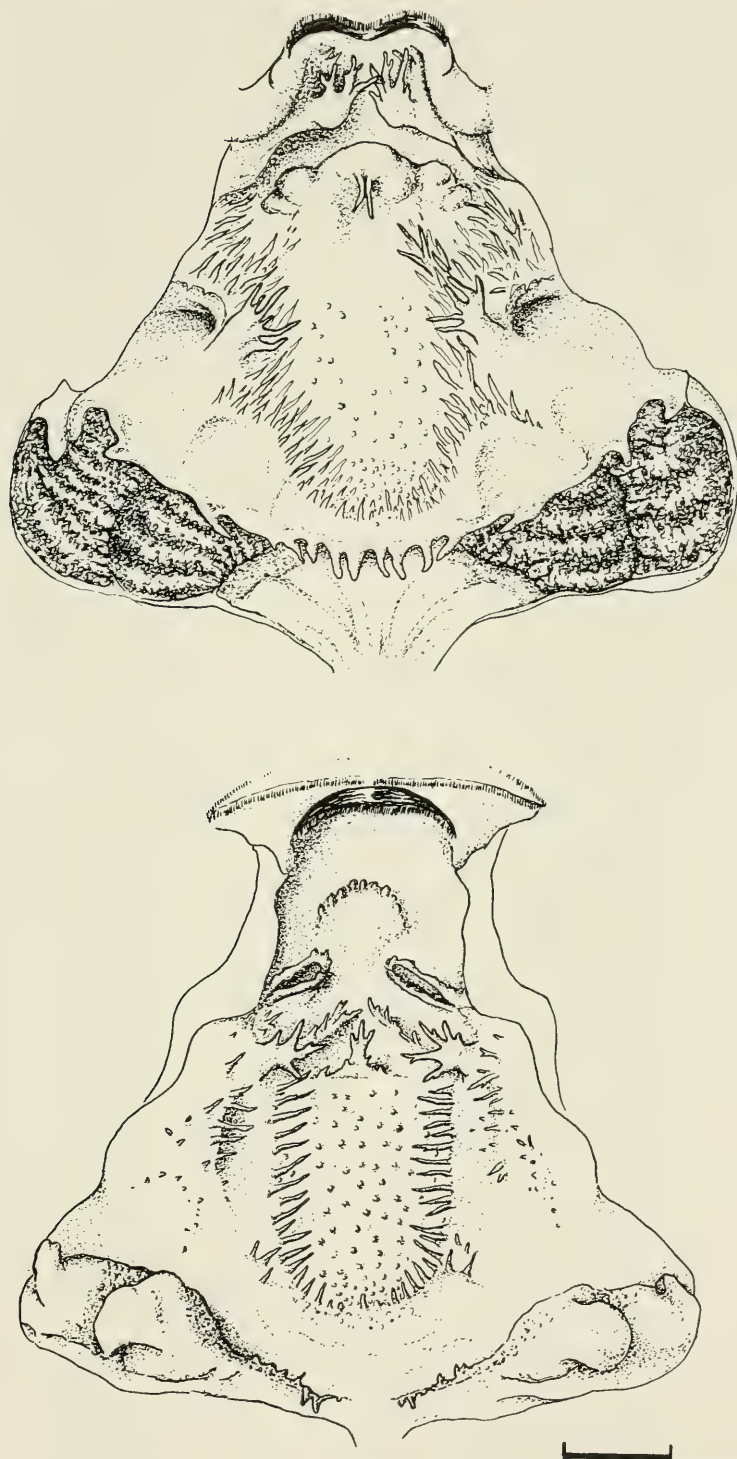


FIG. 30.—Drawings of the floor (above) and roof (below) of the mouth of a *Ptychohyla leonhardschultzei* larva.

projections are clumped together on the velar margin above the glottis. Secretory pits are mostly limited to the surface of the posterior projections. Pits are nearly absent from the velar surface itself except for a very narrow band near the midline.

Ventral pharynx.—The branchial baskets are of typical width to length ratio but have the appearance of being displaced laterally along their posteromedial border. The third filter cavities are reduced in size and partially obscured from dorsal view by the medially imbricating, curved margins of the third filter plates. Filter plates of cb. 1 and cb. 2 are relatively short, while those of cb. 3 are comparatively tall. Counts for number of filter rows fell within the normal range for typical hylid larvae, but those of cb. 1 and cb. 4 were slightly low, while those of cb. 2 and cb. 3 were slightly high. The filter mesh of *P. leonhardschultzei* is quite open, but not as spacious as in *Ptychohyla schmidtorum*. *P. leonhardschultzei* has a typical branching pattern for the filter folds, but all the folds are exceptionally slender, resulting in large filter niches. Branchial food traps and their secretory ridges are not unusual. The glottis is 80% under the velum. It is small and has thin, elevated lips. The laryngeal disc is not visible. The esophageal funnel is of comparable size to that of the more typical hylid larvae examined.

Dorsal buccal.—The buccal roof appears wide anteriorly. The central portion of the prenarial arena is displaced ventrally along the edge of an anteriorly convex arch. This arch is slightly wider than the internarial distance. The edge of the arch is lined with a dozen or so large, blunt pustulations or subpapillar projections and has its greatest depth anteriorly. The internal nares of *P. leonhardschultzei* are elongate. Prenarial papillae are lacking, but about a half dozen pointed pustulations are dispersed over the medial half of the anterior narial wall; the posterior narial walls

lack narial valve projections. Postnarial papillae are located on narrow, obliquely oriented (anteromedial to posterolateral) ridges of moderate size between the anterior end of the internal nares and the median ridge. The tallest postnarial papillae are in the middle of their supporting ridges, where the ridges themselves are tallest. I counted seven postnarial papillae per side. The smaller papillae grade into pustulations at the end of the ridges; the larger are of modest proportion with jagged anterior margins. The median ridge is a small isosceles triangle, with a basal width equal to its height, and with slightly concave sides. It has four pustulations scattered over its anterior surface. There are two or three tiny, pointed papillae in front of the median ridge in the postnarial arena. Laterally, at the posterior end of the ridges supporting the postnarial papillae, are two relatively giant, multipapillate flaps. These flaps, presumed homologues of the lateral ridge papillae, are compressed into the sagittal plane. They have five, attenuate pointed papillae along their lateral margins. Two or three of these papillae have minor bifurcations. Extending directly back from the base of the flaps on each side is a row of tall, thin, pointed papillae that define the lateral limits of the BRA. These rows converge only slightly until they are far back on the buccal roof, where they turn sharply toward the midline. The BRA is thus roughly a rectangle, with rounded corners. It is bound by a total of 34 BRA papillae in this specimen. Three or four of these papillae have a tiny, pointed pustulation near their apices but in general, buccal roof papillae are little ornamented. A hundred or so small blunt pustulations are dispersed within the arena. Ten to twelve tiny papillae, not quite as tall as those in the BRA series, form a secondary line or cluster of papillae lateral to the middle of the arena. Lateral to the posterior end of the arena are small pustulate fields also including a couple



FIG. 31.—Photographs of the floor (above) and roof (below) of the mouth of a *Ptychohyla leonhardschultzei* larva.

of tiny papillae on each side. The glandular zone is not wide. Secretory pits are small in *P. leonhardschultzei*, although they are not atypically dense. Overall, the dorsal velum is of typical size and shape, but it is interrupted medially and its free medial edges are sculptured into a series of small, simple papillae on each side.

Dorsal pharynx.—The pressure cushions are equal to, or larger than, those of more typical hylid larvae. The medial pressure cushions are the larger and rounder of the pairs. The ciliary groove is deep and narrow.

Diagnostic summary.—Tadpoles of this species have the greatest number of buccal floor and buccal roof arena papillae of any species examined and, as such, can be distinguished readily from all other hylid larvae examined.

Acris crepitans Baird
(Fig. 32)

Material.—FMNH 11916 (stage 36, sv. 16.8 mm). Collected 6.4 km W of Fort Worth, Tarrant Co., Texas; March 29, 1931.

Reference.—Stebbins, 1951 (p. 301-304); Heyer, 1976.

External.—Tadpoles of the genus *Acris* have a 2/3 denticle pattern and a sinistral spiracle. Their body form and habits typify the "common" pond tadpole.

Ventral buccal.—*Acris crepitans* larvae are indistinguishable from *H. regilla* larvae in the shape of their mouths and general oral proportions. The few differences between the two species largely correlate with the greater size of *A. crepitans*. The position and shape of papillae on the buccal floor, including the infrarostral, lingual, BFA and the buccal pocket papillae, are identical to *H. regilla*. The same situation holds for pustulations on the buccal floor. The BFA papillae may be slightly taller and more numerous than those of *H. regilla*, but not significantly so. (In the specimen on which this description is based,

there are three lingual papillae. Examination of other *A. crepitans*, however, shows that two lingual papillae are typical and that this individual is abnormal in that feature). The buccal pockets of *A. crepitans* are clearly perforated. The secretory pits on the dorsal margin of the velum are possibly a bit larger than those of *H. regilla*, but the difference is slight and may be accounted for by preservational differences.

Ventral pharynx.—The filter rows fall within the normal range for *H. regilla* of comparable stage; filter rows are a bit wider in *A. crepitans* than in *H. regilla*. Overall, the filter mesh appears slightly less dense in *A. crepitans*. Again this difference is small enough to be ascribable to differences in preservation.

Dorsal buccal.—All major features are as in *H. regilla*; the few distinctions between *A. crepitans* and *H. regilla* are almost all comprehensible as simple augmentations associated with overall increase in size. There are twice as many prenarial papillae in *A. crepitans* as in the average *H. regilla*; the narial valve projections are more attenuate. I counted seven postnarial papillae in oblong (anterolateral to posteromedial) clusters on each side of the midline in this specimen; this is significantly more than in *H. regilla*. At least one of these was bifurcated. A couple of small papillae and a half dozen or so pustulations were within the postnarial arena. The median ridge and lateral ridge papillae are similar to those of *H. regilla*. Additional papillae, anterolateral to the lateral ridge papillae, are present. There are twice as many BRA papillae in *A. crepitans* as there are in *H. regilla*. Ten or more papillae with some associated pustulations occur lateral to the BRA on each side. Evenly dispersed within the arena are well over a hundred medium to small pustulations. The glandular zone is identical to that of *H. regilla*, although it is a bit easier to resolve secretory pits in the one specimen on hand.



FIG. 32.—Photographs of the floor (above) and roof (below) of the mouth of an *Acris crepitans* larva.

Dorsal pharynx.—Pressure cushions can be discerned as two round faint swellings on the posterior surfaces of the dorsal velum on each side. These cushions and the ciliary groove are indistinguishable from those of *H. regilla*.

Diagnostic summary.—Tadpoles of the genus *Acris* are so similar externally, that it is reasonable to consider *Acris crepitans* as representative of the genus.

Acris crepitans tadpoles have a higher number of postnarial papillae than any other larvae examined. There are significantly more buccal roof arena papillae in *Acris crepitans* tadpoles than in *Hyla regilla* tadpoles. Otherwise, the larvae of these two species are virtually identical.

Smilisca sordida (Peters)

(Fig. 33)

Material. — Uncatalogued, author's collection (stage 37, sv. 11.5 mm). Collected singly in clear shallow, but slow flowing water of the Rio Rincon near ten mile mark on the Pacifica Road from Rincon de Osa, Puntarenas, Costa Rica; March 4, 1970.

Reference. — Duellman, 1970 (p. 617).

External.—These tadpoles have a 2/3 denticle pattern and a sinistral spiracle; only a slight ventral shift of the mouth and elongation of the tail distinguishes these tadpoles from typical pond polliwogs. Externally they show few of the modifications characteristic of stream tadpoles.

Ventral buccal.—Anteriorly the floor of the mouth is slightly expanded laterally. The infralabial papillae are cupped flaps of skin no different in size and shape than those of typical pond hylid larvae, but with finely serrated margins rather than papillate "fingers." Lingual papillae are tall. The buccal floor arena is defined by a modest number of papillae, some eight per side. The BFA papillae do not converge strongly toward the midline at the anterior limit of the BFA. The three or four largest

BFA papillae, those directly medial to the ends of the buccal pockets, are fused to their neighbors at their bases. There are single, prepocket papillae on each side, which are relatively tiny and sharply pointed. A dozen or so large pustulations are in the posterior half of the BFA. Fine pustulations are also scattered above the lateral arms of the ceratohyals, among the BFA papillae, and posteriorly behind the arena. This last posterior patch extends laterally to the front of the second filter cavity. Single, tiny papillae are among the pustulations on the ceratohyal arms in front of the second filter cavity. The buccal pockets of *S. sordida* are large, long and more transversely oriented than those of *H. regilla*. They are conspicuously perforated. The free velar surface is large and supported by stiff, long spicules that come close to reaching the velar margin. Posterior projections from the velar surface are long and leptokurtic. The projections associated with the third filter cavities are displaced medially. The projections of both the second and third filter cavities are pointed posteromedially. One or two tall secondary projections are developed next to the relatively deep median notch. Large, conspicuous secretory pits form a thin band on the posteromedial portion of the velar margin. This band is diminished laterally; distal to the second filter cavity the pits are restricted to the marginal projections of the velum.

Ventral pharynx.—The branchial baskets viewed from above are typical in size and shape. They are, however, not particularly deep and individual filter plates are imbricated to a great extent. The third filter cavity is reduced in width. In terms of other characters of the filters, viz. the length to height ratio of the filter plates, number of filter plates on the rows, pattern of the filter folding, density of filter mesh, etc., *S. sordida* is indistinguishable from more typical hylid larvae. Branchial food traps are necessarily shallow because of the shal-

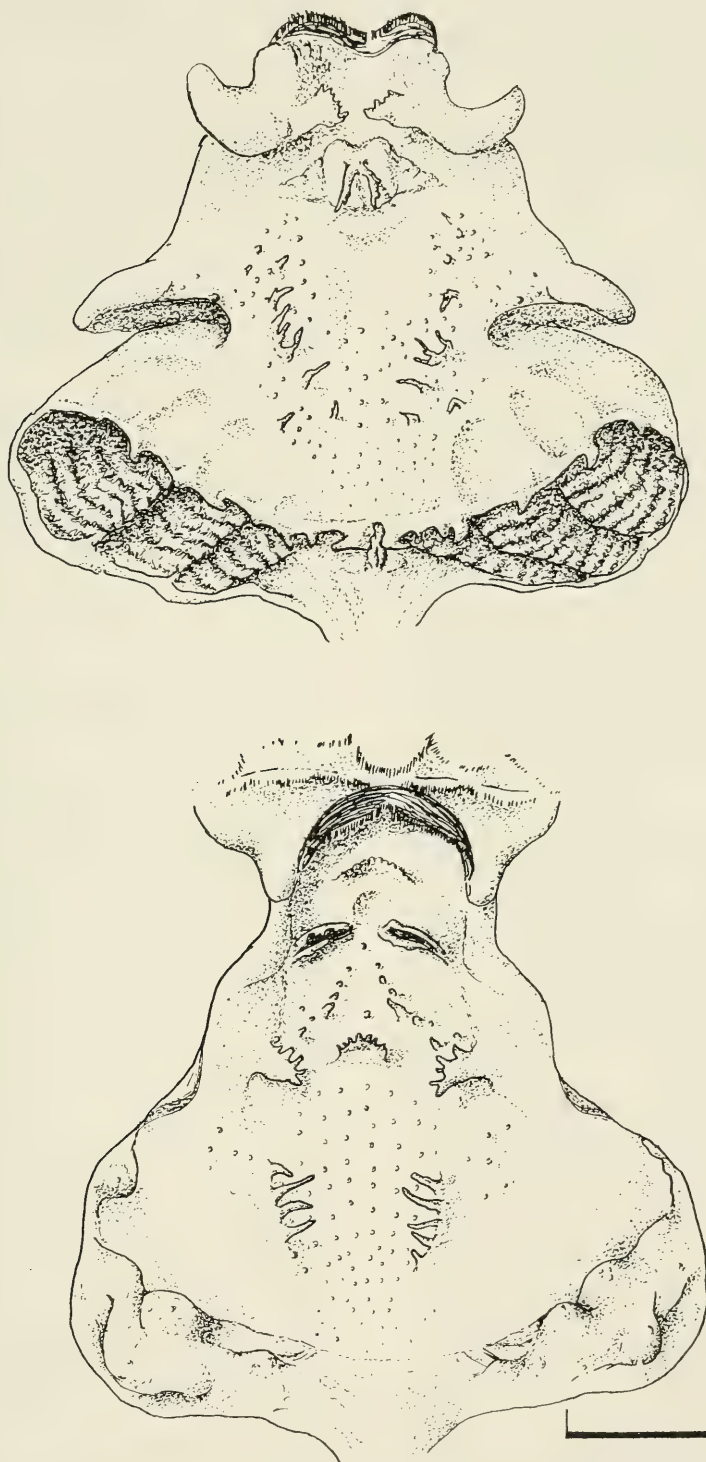


FIG. 33.—Drawings of the floor (above) and roof (below) of the mouth of a *Smilisca sordida* larva.

lowness of the branchial baskets, but, because of the larger free velar surface, the actual area covered by secretory ridges is not reduced. The secretory ridges are similar to those of typical pond larvae. The glottis is typical. The laryngeal disc is not visible. The esophageal funnel is a bit broader but no larger in *S. sordida* than in the reference hyalid larva.

Dorsal buccal.—The buccal roof has the same length to width ratio as *H. regilla*, but a slightly more square, less triangular shape. The central portion of the prenarial arena bulges ventrally. On the surface of this shallow bulge is an anteriorly directed pustulate arch. The arch is twice as wide as the internarial distance. The internal nares of *S. sordida* are more elongate and obliquely oriented than in a typical pond larva. Prenarial papillae are lacking, but many tiny, pointed pustulations line the whole length of the low, anterior narial walls. The posterior narial walls lack narial valve projections. Postnarial papillae, two on one side, four on the other are small, simple, blunt projections. These are in obliquely oriented (anteromedial to posterolateral) lines that include an equal number of evenly spaced pustulations. The reduced median ridge is as tall as it is wide and has a peaked rather than horizontal ventral margin. This ventral margin is lined with many fine serrations, and there are single isolated pustulations on the anterior surface of the median ridge. Extending back from the ends of the postnarial papillae row, posterolateral to the median ridge, are large, nearly longitudinally oriented flaps. These are presumed homologues of the lateral ridge papillae. Each flap is tallest posteriorly and deeply notched, so that it has at least five sharp peaks along its margin plus a couple of minor, pointed pustulations. Continuing posteriorly in line with the long axes of the lateral flaps are single rows of BRA papillae on each side. These are slender, pointed papillae of modest size, num-

bering five per side. There is a gap equal to a seventh of the length of the buccal roof separating the first BRA papillae from the posterior edge of the lateral flaps. The BRA papillae rows converge only slightly towards the midline and outline a rather elongate buccal roof arena. There are sixty or more pustulations within the arena; their greatest concentration is posterior. Directly lateral to the gap between the lateral flaps and the most anterior BRA papillae are small clusters of four or five pustulations and one tiny papilla per side. The glandular zone is slightly shortened both medially and laterally compared with more typical pond larvae. The secretory pits are not unusual in any way. The dorsal velum is short and has a broad gap across the midline. The more medial limits of the velum have a pustulate margin.

Dorsal pharynx.—Pressure cushions are of comparable length to those of *H. regilla* but are necessarily smaller because of the decrease in free velar surface. The ciliary groove is narrow.

Diagnostic summary.—Because only one species of *Smilisca* was examined internally, it would be premature to attempt to diagnose the genus. The *Smilisca sordida* group of *Smilisca* includes stream breeders; it is a reasonable hypothesis, however, that the oral cavity of *S. sordida* larvae will resemble that of other stream *Smilisca* tadpoles more than it will resemble that of the larvae from the non-stream breeding *Smilisca baudinii* group. On the other hand, it is possible that with such slight differences between typical pond larvae, such as *Hyla regilla*, and *Smilisca sordida*, other species of *Smilisca* may not be distinguishable from *S. sordida* in larval oral anatomy. The following are a few of the oral features in which *Smilisca sordida* larvae differ from *Hyla regilla* tadpoles: lingual papillae taller; spicules stiffer and longer; velar marginal projections longer; filter plates more im-

bricated; branchial food traps shallower; pressure cushions smaller.

Agalychnis callidryas (Cope)
(Fig. 34)

Material.—Author's collection (3 specimens: stage 35, sv. 19.9 mm; stage 37, sv. 18.6 mm; stage 39, sv. 19.2 mm). Collected in massive swarming schools in the "Caiman" pond, by Pacifica Road, 9.7 km south of Rincon de Osa, Puntarenas, Costa Rica; March 4, 1970.

Reference.—Duellman, 1970 (p. 107-108).

External.—Tadpoles of the genus *Agalychnis* all have an elongate, filamentous tail. Their eyes are far lateral, their mouths are directed anteriorly or anteroventrally; the spiracle is just left of the midline. The denticle pattern is, however, the common 2/3 arrangement.

Ventral buccal.—The floor of the mouth is anteriorly broader and posteriorly more elongate than in typical hylid larvae. A single, tiny, soft spur is present on the infrarostral cartilage posterior to the edge of the beak but in line with the keratinized cutting edge on each side. The infralabial papillae all lie well medial to these spurs. Three to five infralabial papillae per side are present. The largest papilla on each side is always the most medial. These more medial papillae are tall, tapered, and round to slightly oval in cross section. They curve directly anterad. The smaller, more lateral papillae are round in section and do not curve anterad. These more lateral infrarostral papillae form an anterior to posterior line or cluster, with the most anterior papilla slightly larger than the more posterior ones. The largest medial papillae are 1.5 to 2 times taller than any of the lateral papillae. All papillae are unbifurcated. The two lingual papillae are so close to each other and to the midline that they effectively share a common base. The buccal floor arena is outlined by two posteriorly converging lines of papillae. Anteriorly these rows flare out laterally

into a dense field of numerous tiny pustulations and subpapillae above the body of the large ceratohyal on each side. Six to nine ($\bar{X} = 7.5$) BFA papillae make up the row on each side; none are bifurcated. The posterior four to five papillae are equal or subequal in size and shape. These are in a perfectly straight row. The papillae at the beginning of the series are similar, but smaller and not in such straight lines. Anteriorly two small papillae lie inside the arena. These are next to and parallel the main papillae row. Sixty or more tiny pustulations cover the buccal floor. They are most concentrated posteromedially in the BFA and laterally above the ceratohyals. There are no isolated prepocket papillae *per se* but a few small papillae, not separable from the pustulate lateral field at the anterior end of the BFA papillae rows, may be homologous to the prepocket papillae in other species. The buccal pockets may be perforated in the stage 37 specimen, but are not evidently open in either the stage 35 or 39 specimens; a consistent species pattern cannot be resolved with the small sample at hand. The anterior to posterior length of the free velar margin over the filter cavities is larger, and the supporting spicules longer, than in most other hylids. The margin of the ventral velum has four posteriorly directed acute peaks. The peaks, which are most obviously homologous with the velar crenulations normally above the third filter cavity in other hylids, are displaced medially. Several paired auxiliary projections in this region effectively produce a field of papillae trialing off the edge of the velum above the glottis. Single, broad crenulations are present on the velar margin between the peaks above filter cavities 1 and 2; these are also posteriorly directed. The pitted glandular zone on the dorsal surface of the ventral velum has a sharply defined anterior margin. The glandular tissue is densest on or near the major peaks and tends to thicken the edge of the velum.

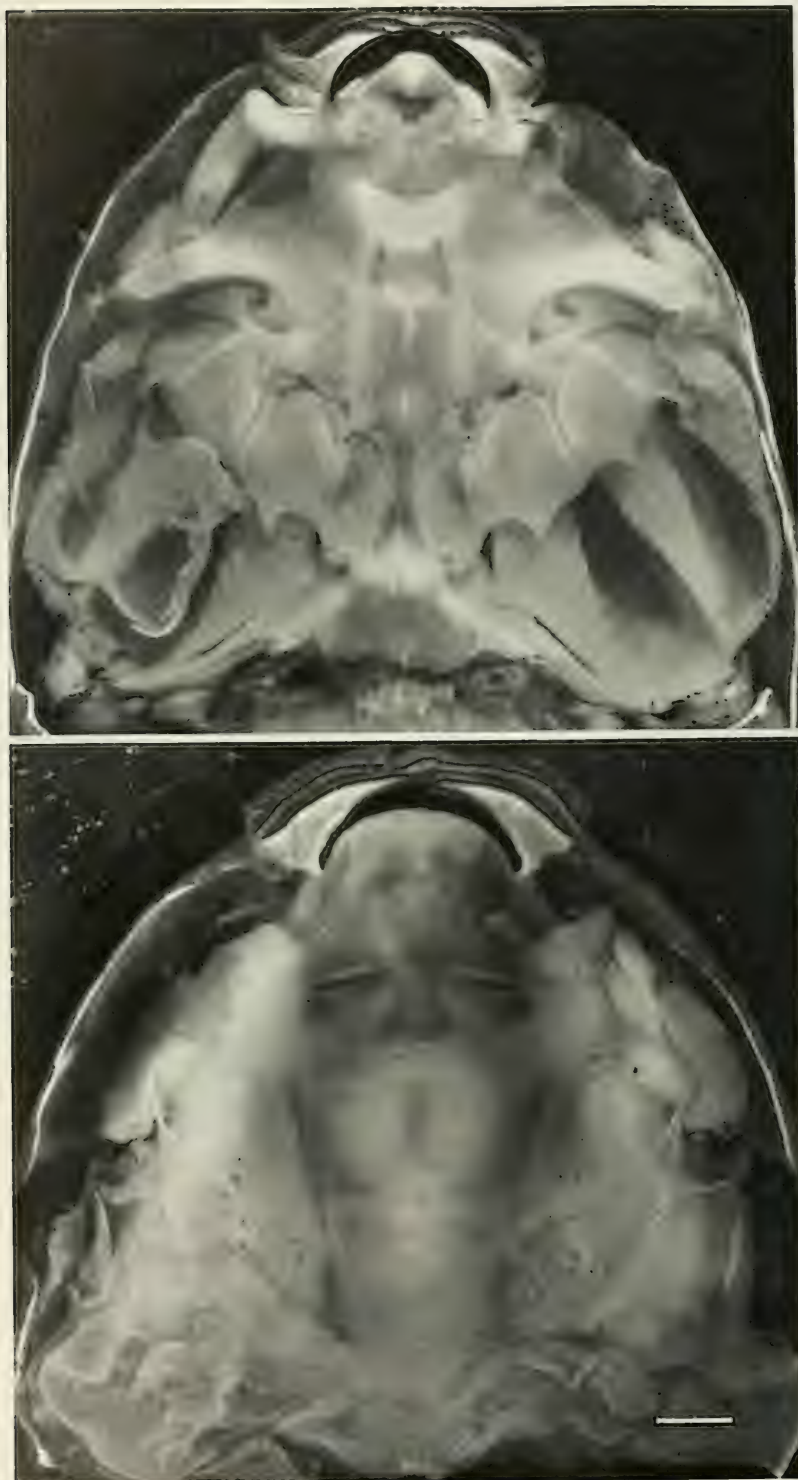


FIG. 34.—Photographs of the floor (above) and roof (below) of the mouth of an *Agalychnis callidryas* larva.

Ventral pharynx.—*Agalychnis* is characterized by substantially larger branchial baskets, a greater amount of filter surface, and a finer filter mesh than any other hylid examined. Filter plates are longer and particularly taller than in *H. regilla*, although the length to width ratio for the branchial baskets *in toto* do not differ; the additional filter surface in *Agalychnis* is taken up in increased curvature and imbrication of the filter plates. The major axis of the second filter cavity projects back from the midline at a very acute angle. The ceratobranchials and the filter plates that they support are strongly bowed outward. Filter plate 1 is so curved that in cross section it circumscribes half a circle. The dorsal margins of the filter plates on cb. 2 and cb. 3 are not straight, but arch upward to a peak just behind the edge of the ventral velum. These plates are strongly imbricated toward the midline causing the filter cavities, particularly cavity 3, to be almost completely encircled by filter epithelium. The number of full filter rows on each plate are exceptionally high; they range as follows: cb. 1 = 11-13, cb. 2 = 12-15, cb. 3 = 12-13, cb. 4 = 8-9. The filter mesh is far tighter than in other hylids. Secondary filter folds are numerous and dense. Filter rows do not simply terminate at the ventral borders of the filter plates, but interdigitate with the rows on the opposite filter plates, completely obscuring the gill slits. Partial, tapered filter rows project deeply ventrad between normal full rows and fill any spaces between the full filter rows. Filter canals are virtually complete tubes, rarely visible without displacement of the filter rows. Narrow and closely packed secretory ridges are readily visible on the ventral surface of the ventral velum. The ridges appear discontinuous directly under the spicule of cb. 2. Branchial food traps cover a large proportion of the anterior surface in the filter cavities extending down the medial anterior wall of each cavity. The glottis

appears fully developed, although not large. The glottal lips are raised on a strongly developed anterior to posteriorly directed ridge. The papillate midportion of the ventral velum margin makes it impossible to estimate, in any consistent way, the amount of glottis obscured by the velum. The esophageal funnel is of relatively narrow profile.

Dorsal buccal.—The roof of the mouth is quite wide anteriorly. In the center of the large prenarial arena is a single, darkly staining, semicircular (concaved posteriorly) low ridge. Evenly spaced on the top of the ridge are short, knobby projections, 4 to 7 per side. Posterolaterally these are mere pustulations, but anteromedially they develop into unusually shaped, low nodular papillae. There is a faint medial gap in the ridge. Medially within the semicircle, are one or two more typical, prenarial pustulations. The internal nares are not unusual in shape, except that the openings to the olfactory capsule are small and far lateral. There are no distinct prenarial papillae, although the raised anterior wall of each naris is rugose in texture, particularly medially. The narial valve projection is shorter than in more typical hylid larvae. Between the nares and the median ridge lie three distinct papillae on each side. These papillae all arise from a common straight ridge oriented anteromedially to posterolaterally. On each side the most anterior of the three papillae lies directly behind the narial valve projection. This is a very large, conical, acutely pointed papilla. It is taller than the narial wall and projects anteriorly under the narial valve projection in one specimen but a bit more medially in the other two. The middle papilla in the series is the smallest. It is a simple, tiny, finger-shaped papilla aligned behind the middle of the nares and about halfway back in the narial arena. This papilla is directed anteriorly. The last papilla on the ridge is a simple, stout, cone one-half to one-third the size of the largest

anterior papilla. This last papilla aligns itself behind the lateral end of the nares and two-thirds of the way back in the narial arena. It is oriented medially. In two of the three specimens, postnarial papillae show some very fine pustulations along their most anterior margins. A single, basal bifurcation was found asymmetrically on the third papilla in one of the specimens; elaborate bifurcations of the posterior narial papillae are probably rare in this species. The last papilla in the posterior narial papillae row may be homologous to the lateral ridge papillae; however, they are displaced a bit forward and because they sit on a common ridge with the other papillae within the narial arena they are considered here part of the postnarial papillae series. There are no other papillae directly lateral to the median ridge. The median ridge is a transverse flap, shaped like an isosceles triangle. It is positioned slightly anterior to the middle of the buccal roof. The ridge has a basal width one to two times its height and a single or occasionally bifurcated apex. No secondary anterior fringe is present. Between seven and ten pustulations are scattered within the postnarial arena. The buccal roof arena covers the flat, medial one-third of the buccal roof. The arena is bound laterally by two patches of simple, moderately small, finger-like papillae, seven to nine per side. The patches trend antero-laterally to posteromedially. Posteriorly, the patches tend to narrow into single rows. The papillae do not vary much in size, but the largest ones are generally in the middle portion of the patches. None of the papillae are bifurcated. Within the arena are approximately eighty randomly dispersed, darkly staining spots, almost too small to be called pustulations. These are absent outside of the arena. A secondary cluster of lateral roof papillae appears on each side about halfway between the main BRA papillae patches and the lateral edge of the mouth. The one to six pa-

pillae in these lateral "clusters" are, on the average, one-fourth the height of the main BRA papillae. The glandular zone is well defined and made up of conspicuous secretory pits, which are large, round and abutting. These extend well over the dorsal velum and onto the pressure cushions. They are densest on the edge of the velum. The anterior margin of the glandular zone is strongly scalloped. Two lateral swells on each side match perfectly the anterior limits of the free edge of the ventral velum over filter cavities 2 and 3 below. The dorsal velum is divided on the midline by a substantial gap. The medial margins of the dorsal velum may point towards each other or the edges may turn posterior to form a funnel that parallels the esophageal funnel. Laterally, the edge of the dorsal velum is thick, glandular, and not curled. The velum is relatively and absolutely smaller than in more typical hylid larvae.

Dorsal pharynx.—The pressure cushions are comparatively huge, obliquely oriented ovals, extending well down into filter cavities 1 and 2. The medial cushions are about three times as wide as the lateral cushions and twice as tall. The ciliary groove is relatively narrow and deeply entrenched.

Diagnostic summary.—Of the species examined in detail, *Agalychnis callidryas* differs from all other hylids (*sensu lato*) in having massive branchial baskets, dorsally arched filter plates, and an extremely dense filter mesh. cursory examination of other species in the genus of *Phyllomedusa* suggest that the diagnoses will not distinguish *A. callidryas* from other middle American phyllomedusine tadpoles.

CENTROLENIDAE

Centrolenella fleischmanni (Boettger)
(Fig. 35)

Material. — Uncatalogued, author's collection (R. W. McDiarmid Field No. 6865 "clutch #3") (stage 30, sv. 6.9 mm). Raised from eggs. Monteverde,

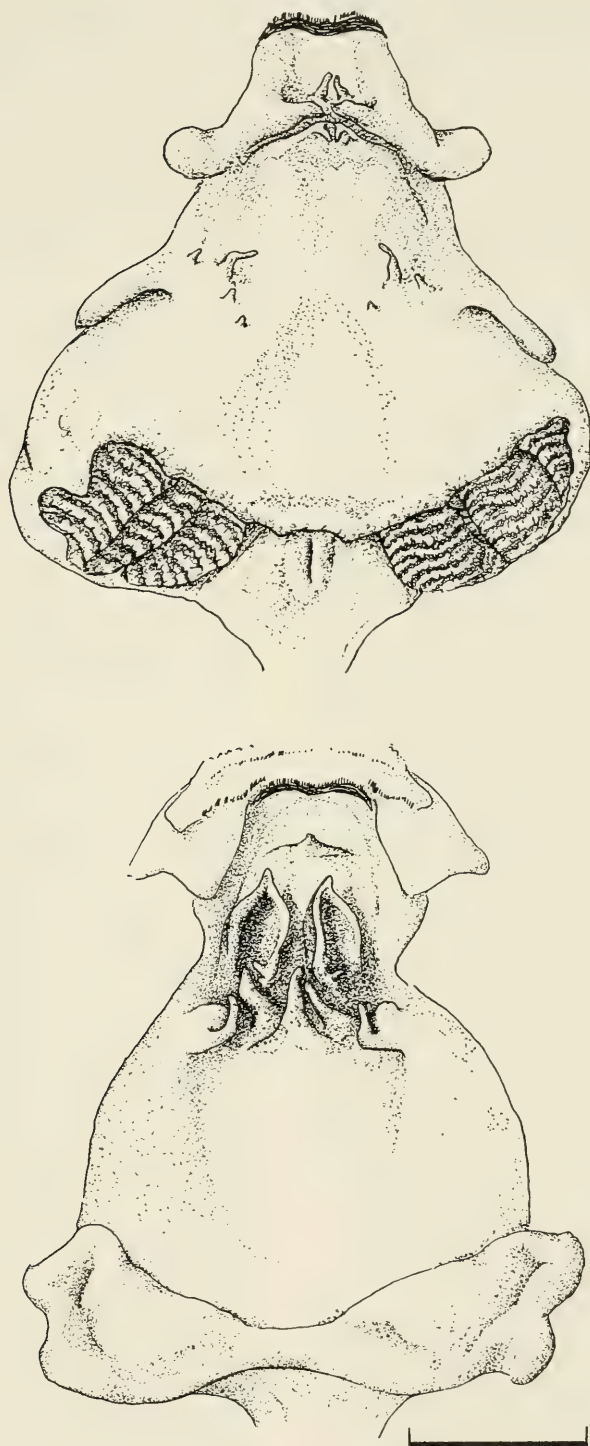


FIG. 35.—Drawings of the floor (above) and roof (below) of the mouth of a *Centrolenella fleischmanni* larva.

Puntarenas Prov., Costa Rica; collected July 4, 1971; preserved Aug. 20, 1971.

Reference.—Starrett, 1960; Villa, 1971; Heyer, 1976.

External.—The tadpole of *Centrole-nella fleischmanni* is extremely elongate, with a tail more than twice as long as its body. The denticle pattern is $2/3$ and a single, sinistral spiracle is located $3/4$ th the way back on the body. The external nares are tiny pores; the eyes are small, deepset and directed dorsally.

Ventral buccal.—Internally the floor of the mouth is of the overall triangular shape of most tadpoles; however the oral orifice itself is narrow and the buccal surface behind the buccal pockets is exceptionally elongate. There are two pairs of infralabial papillae; a medial pair adjacent to the midline and a lateral pair placed more typically over Meckel's cartilage. The medial papillae are simple, tall, but blunt structures that overlap on the midline. The lateral pair are small, anteroposteriorly flattened flaps, which are slightly concave anteriorly; one has slight marginal pustulations, but they both lack secondary papillae. The base of the lingual papillae is a transversely oriented ridge and on its apex is a transverse row of four small lingual papillae. There is but one BFA papillae on one side, four on the other; these are displaced far laterally and barely define an arena. The papillae lack secondary pustulations; they are flattened against the buccal floor and have slightly knobby crowns. Most of the buccal floor lies behind these papillae and completely lacks topographic relief. Papillae and pustulations are also absent from within the BFA or in the region anterior to the buccal pockets. The prepocket region is small. The buccal pockets are shallow creases with a strongly oblique orientation. Buccal slits appear (?) patent. The free velar surface is gently curved, lacking projections. The median notch is very weak and shallow. A thin zone of glandular tissue is evident over the margin.

Ventral pharynx.—Seen from above the ventral pharynx is long laterally and narrows sharply toward the midline. The result is that the branchial baskets appear relatively triangular in shape. The baskets are extremely shallow. The filter plates are short and only slightly imbricated. The tallest plate is the second. The fourth filter plate is strongly arched in the transverse plane. Filter rows are well organized along the dorsal margins of the filter plate particularly the second filter plate; ventrally the filters become less organized and have a puffy, spongy-like texture. It is possible to discern secondary and occasionally tertiary filter folds on some of the filter rows but others appear relatively disorganized, lacking an obvious branching pattern. Despite the fact that the higher order filter folds are not always visible, there are no large spaces between filter rows; filter canals appear to be relatively narrow, shallow slits. Counts for filter rows run: cb. 1, 9; cb. 2, 15; cb. 3, 11; cb. 4, 10. These should be considered minimum estimates as it was very difficult to collect these data on such a small specimen. The gill filters are unusual in that they show such a broad range of structural organization. The light grainy texture characteristic of secretory tissue is evident on the short surface of the branchial food traps; however, even at $100\times$, well organized secretory ridges could not be discerned in this region and may be lacking in the species. The glottis is distinct with heavy lips. An elevated laryngeal disc is absent at this stage. The esophageal funnel is of comparable shape to that of most other anurans examined.

Dorsal buccal.—The buccal roof has the basic triangular shape typical of other anurans. The prenarial arena is narrow, long and nearly vertically oriented, a reflection of the ventral position of the oral orifice. There is one stiff, enlarged triangular projection which extends down from the posterior portion of the prenarial arena. It has a slightly

compressed, transversely oriented base. There are no other papillae or pustulations in the prenarial arena. The internal nares are large, longitudinally oriented, open pits. The long median walls of these vacuities virtually meet on the midline. The prenarial papillae are points that extend forward from the front of the tall narial walls. Narial valve projections are lacking. The narial walls on each side circumscribe a large shallow narial depression (Jacobson's organs?) at the base of which is a small slit whose margins completely abut. Because of the small size of the specimen, complete exploration was impossible, but these slits appeared to be patent internal narial openings. The postnarial arena is extremely small and contains a single sharp papilla located on the midline in the middle of the arena. It is hidden from ventral view by a simple, triangularly shaped median ridge that is adpressed against the buccal roof. Although the median ridge is not large, the narial depressions are so long that the apex of the median ridge projects between the posterior portions of the internal nares. Immediately to the sides and slightly anterior to the median ridge lie two pointed papillae, presumed homologues of the lateral ridge papillae. They fit in the space between the median ridge and the posterior wall of the internal nares. A short distance lateral and slightly posterior to each lateral ridge papilla lies a single obliquely oriented, posteromedial to anterolateral compressed flap on each side. The homologues of these projections are uncertain. Whereas they are too far posterior to be associated with the median ridge, they are too far anterior to be obvious buccal roof papillae. Each flap has a terminal, anterolateral, fingerlike projection that points anteriorly, and a more posteromedial cusp similarly directed along the same edge. All of the structures so far described lie in the anterior half of the buccal roof. Papillae and pustulations of any sort are lacking from

the remainder of the buccal roof. The boundaries and general proportions of the glandular zone could not be discerned in this specimen and a distinct glandular zone may be lacking in this species. The dorsal velum is short, uncurled, anteriorly directed, and continuous across the midline.

Dorsal pharynx.—On the posterior surface of the dorsal velum are two extremely slight swellings on each side, the only evidence of pressure cushions. The medial swellings are larger and more obvious. The ciliary groove is a shallow broad channel.

Diagnostic summary. — Many fine features of papillae pattern and shape are unique in this form compared to the other larvae described. The combination of the following major features, however, readily serve to distinguish the oral cavity of this species from all others: long buccal floor and roof behind buccal slits and median ridge respectively, with both areas lacking papillae and pustulations; shallow branchial baskets; very large, longitudinally oriented internal narial depressions; four lingual papillae.

DENDROBATIDAE

Colostethus subpunctatus (Cope) (Fig. 36)

Material.—MVZ 63199 (stage 34, sv. 11.7 mm). Collected from small rain pool at 2650 m elevation Bogotá, Cundinamarca, Colombia; Oct. 15, 1950.

External.—*Colostethus subpunctatus* larvae have flattened venters and dorsally directed eyes. The spiracle is sinistral and denticle formula is 2/3.

Reference.—Stebbins and Hendrickson, 1959.

Ventral buccal.—The floor of the mouth is generally similar to that of many pond tadpoles. In addition to weak spurs, directed anteriorly at the very margins at the oral orifice, there are three major papillae associated with the infralabial region. The smallest infralabial papillae are two blunt projec-

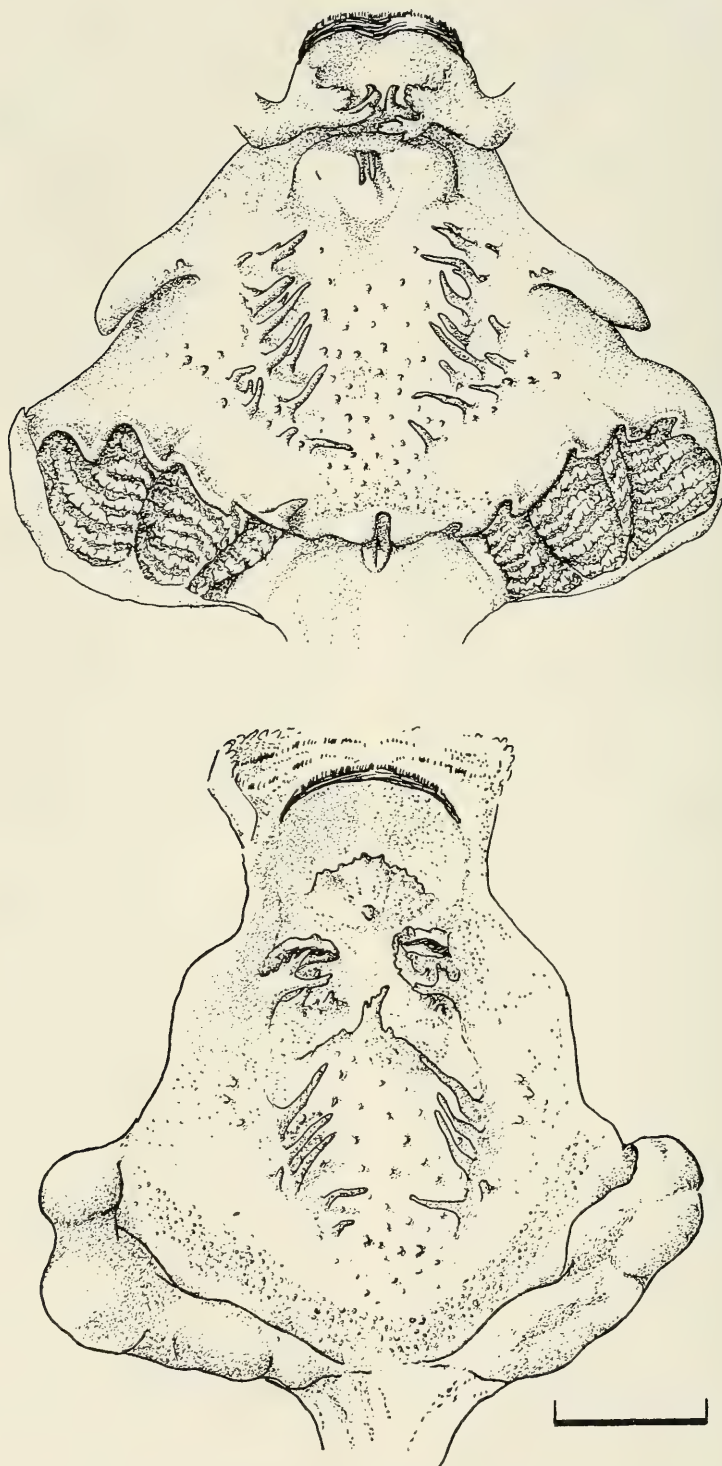


FIG. 36.—Drawings of the floor (above) and roof (below) of the mouth of a *Colostethus subpunctatus* larva.

tions arising from the posterior floor of the infralabial region. Their bases abut on the midline. In the typical position for infralabial papillae in other species, arise transversely compress large bifurcate palps with secondary, small, marginal pustulations. The tips of these palps touch on the midline. The third pair of infralabial papillae arise from the anterolateral edge of the large pair just described. These are flaps compressed in the transverse plane. They are nearly as wide as the previously described pair, but not as tall. They have several marginal serrations, but lack secondary papillae. The two lingual papillae are tall. The buccal floor arena is well defined by nine papillae on one side and ten on the other. The arena is relatively narrow and the BFA papillar rows have a slightly oblique (anterolateral to posteromedial) orientation. BFA papillae are similar to those in most pond tadpoles; however, they lack extensive marginal papillations and are noticeably taller and more attenuate. One or two small papillae lie anterior to the medial margin of the buccal pockets. There is a weak field of pustulations in the posterior two thirds of the BFA. Buccal pockets are more obliquely oriented than in *H. regilla*. Large mucosal folds from the posterior walls obscure the base of each buccal pocket. The pockets are of average depth and may be perforated on one side in this specimen. The free velar margin is of average length, but relatively thick and inflexible. Tiny, but dense, secretory pits can be resolved at 50 \times lining the free edge of the velum. The free edge is strongly sculptured with posteromedially directed cusps above the second and third filter plates and additional posteriorly directed cusps above the fourth filter plates. There is a very deep, distinct median notch.

Ventral pharynx.—The branchial baskets are of comparable size and shape to those of typical pond tadpoles. The filter plates, however, are strongly imbricated medially and the medial gap be-

tween the left and right branchial baskets is very large. Filter rows count run 8, 9, 9, 5—similar to that of typical pond tadpoles. The filter mesh is low in density. Neighboring filter rows do not abut, except at their ventral extremes, and partial filter rows are short; thus leaving the filter canals as large open channels. Many of the filter rows lack tertiary or higher order folds, particularly in the small third filter cavity. The branchial food traps are relatively shallow. At 50 \times magnification a weak pattern of transversely oriented ridges can be seen on the ventral surface of the ventral velum. The glottis is completely exposed in the median notch. It is slightly elevated and has distinctive lips; however, it is quite small in all dimensions compared to the overall size of the buccal cavity in this tadpole. The esophageal funnel is very large.

Dorsal buccal.—In general proportions the roof of the mouth is similar to that of pond tadpoles. There is large prenarial arena; from the middle of the arena descends a broad, anteriorly directed, pustulate arch. Halfway between this structure and the internal nares lies a single large pustulation on the midline. The internal nares have a relatively horizontal orientation with a heavy, thick anterior wall, that lacks prenarial papillae. The posterior narial valve has a weak narial valve projection. Aligned in a row in the postnarial arena, parallel to the internal nares, run 4 robust papillae on each side. The most posterior of these lies lateral to the median ridge and may be the homologue to the lateral ridge papilla. These are transversely flattened bifid structures. All of the papillae associated with the postnarial arena including the median ridge have pustulate anterior margins. The smallest postnarial papillae is most anterior. The median ridge is a simple, triangular flap of average size. The buccal roof arena is defined by five, extremely attenuate papillae on one side and four on the other. A few subpapillate projections

arise far lateral to the buccal roof. There are several dozen barely visible pustulations distributed within the BRA. The glandular zone has a very distinctive "V" shaped anterior margin with large conspicuous secretory pits. Posteriorly the secretory pits tend to become much smaller, denser, and less distinct, until one reaches the regions of the pressure cushions, where they again become large and conspicuous. The free velar edge is short, discontinuous on the midline. The medial limits of the velar margin have two or three small, simple papillae.

Dorsal pharynx.—The dorsal pharynx was damaged in dissection, but enough of the pressure cushions were preserved to indicate that these are relatively shallow bulges with the lateral cushion far more distinct than the medial. Details of the ciliary groove were not preserved.

Diagnostic summary.—No single feature distinguishes these larvae from others examined; however, the following characters, in combination easily diagnose the oral cavity of *C. subpunctatus* larvae: 3 pairs of infralabial papillae, BFA and BRA papillae very tall, branchial baskets widely separated, filter plates strongly imbricated but filter mesh weak, glottis small, secretory pits large.

Colostethus nubicola (Dunn)

(Fig. 37)

Material.—Author's collection, uncatalogued (stage 34.5, sv. 8.3 mm). Collected under leaves in small side pools off of a tributary to the Rio Aquabiena, behind Tropical Science Center, Rincon, Osa Penn., Costa Rica; March 8, 1970.

Reference. — Dunn, 1924; Savage, 1968; Heyer, 1976.

External.—*Colostethus nubicola* larvae have an umbelliform, denticle-free, oral disk, directed anteriorly in my specimens. The anterior surface of the disk is pustulate; the nonmuscular portion of the tail is slight; the spiracle is lateral.

Ventral buccal.—The floor of the mouth is broad; the oral orifice wide. The lower beak is directed dorsally and

displaced posteriorly in relation to the tongue anlage. As a result the lingual papillae lie directly medial, rather than posterior, to the major infralabial papillae. The more medial infralabial papillae are small, robust, blunt projections arising from the base of the keratinized beak at the anterior limit of the mouth. The larger, infralabial pair, in a more typical position for infralabial papillae, are complex bifurcated structures. They are directed medially but do not come into contact or touch the interceding lingual papillae. These infralabial papillae have a cupped dorsal portion with the hollow of the cup pointing posteriorly. The lower portion is a single blunt projection, directed medially. The infralabial papillae are fleshy, stiff structures that lack additional surface pustulations or papillae. The buccal floor arena is exceedingly broad. Two, soft, longitudinally oriented swellings arise from the buccal floor anterior to the buccal pockets. These run approximately from the back of the infralabial region to the medial corner of the buccal pockets and define lateral boundaries for the BFA. The posterior half of the BFA is defined by conventional rows of typical papillae; however, these rows continue laterally as small papillae in front of the buccal pockets. I counted five BFA papillae on each side. Assorted pustulations occur in the posterior portion of the BFA and on the buccal floor directly anterior to the buccal pockets. The buccal pockets have a large, fleshy posterior flap. They are deep and appear perforated in this specimen. The free velar surface is long and supported by long, conspicuous spicules. The free edge is similar to that of *Colostethus subpunctatus*; there are small posteriorly directed peaks on the free velar edge over the second filter plate and medially directed peaks over the third filter plate. A tiny cusp, pointed posteriorly on each side, is aligned over the top of the fourth filter plate. There is a well-developed medial notch. Secretory tissue exposed

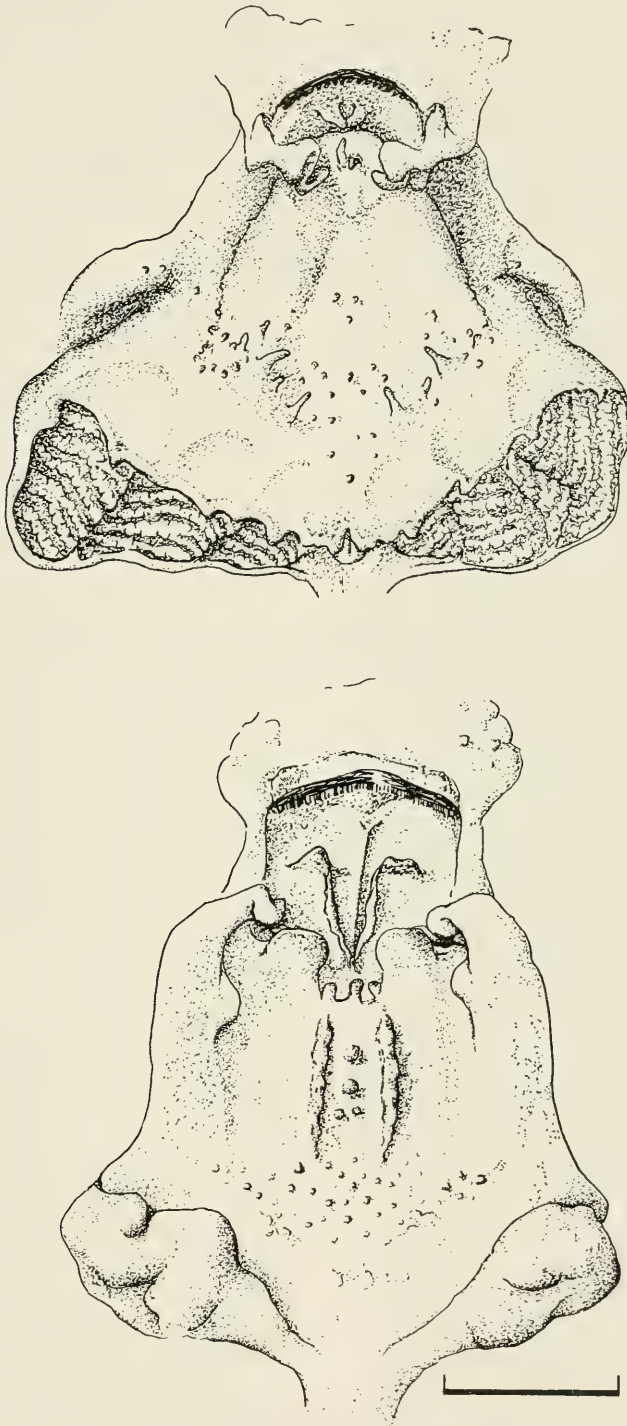


FIG. 37.—Drawings of the floor (above) and roof (below) of the mouth of a *Colostethus nubicola* larva.

on the dorsal side is similar to that of *C. subpunctatus*.

Ventral pharynx.—Branchial baskets are similarly shaped to those of *C. subpunctatus*; however, the second filter plate is not as tall while the third is slightly taller and has a curved dorsal margin which virtually covers the third filter cavity. Counts for filter rows are 7, 8, 8, 5 for cb. 1-4; these are slightly less than those of *Hyla regilla* at a comparable stage. The filter density and fold pattern is almost indistinguishable from that of *C. subpunctatus* and less dense than that of typical pond tadpoles. Tertiary filter folds are less well developed in this dendrobatid than in the one previously described. Filter canals are very open channels. The branchial food traps are shallow, but cover a large area due to the large free surface of the ventral velum. Secretory ridges could barely be discerned at 50 \times magnification. The glottis is two thirds covered by the ventral velum. In size and shape it is similar to *C. subpunctatus*. The esophageal funnel is relatively broad but not as large as in *C. subpunctatus*.

Dorsal buccal.—The buccal roof is elongate. The prenarial arena is flat and very conspicuous. A narrow sharp ridge runs from the anteromedial margin of the dorsal beak two-thirds of the way back in the prenarial arena. A papilla descends on each side of the prenarial arena about halfway between the upper beak and the nares. Each is transversely compressed with a gently curved, free, ventral edge. Medially the ventral edge for each papilla continues along the buccal roof as a posteriorly directed ridge that converge on a tiny papilla midway between the internal nares. There are no pustulations or additional structures in the prenarial arena. The internal nares are oriented transversely. Their anterior walls are shallow and lack projections or papillations of any sort. There is a short, but distinct, narial valve projection far medial on the posterior edge of the narial valve. A glo-

bous projection arises from the lateral wall of the buccal roof on each side. Each fills the space between the narial valve projection and the lateral margins of the nares. The postnarial arena is extremely small and is bounded posteriorly by a small, truncated papilla which on topographic grounds may be the homologue of the median ridge. No other papillae are present in the postnarial region except for a giant fleshy flap behind each narial valve projection and a pustulation (homologue of lateral ridge papilla) immediately lateral to the median ridge on each side. The flaps just described is the largest structures on the buccal roof. They are transversely compressed with a rounded, free edge that covers the medial half of the internal nares on each side. The next largest structures associated with the buccal roof are simple, soft, oval projections arising from the far lateral walls of the buccal roof directly posterolateral to the large flaps just described. These more lateral structures may be homologues of lateral roof papillae in more typical anuran larvae. A faint, longitudinal ridge runs the length of the middle third of the buccal roof on each side. These structures vaguely define the lateral margins of a narrow BRA. There is a field of some twenty to thirty small pustulations in the region directly behind and medial to the ridges, but no papillae of any sort are present on the buccal roof behind the median (ridge) papillae. The glandular zone is large, but its anterior margin is poorly defined in this specimen. Individual secretory pits could not be discerned. The dorsal velum is of comparable size to that of more typical pond tadpoles. It is barely continuous across the midline.

Dorsal pharynx.—Pressure cushions are distinct. The lateral cushion is smaller and more elongate along an anterior-posterior axis. The medial cushion is a larger, more oval bulge. The ciliary groove was not preserved in dissection.

Diagnostic summary. — *Colostethus nubicola* is very different from *C. subpunctatus* in its buccal anatomy but it shares many features with other funnel-mouthed larvae from other families. However, its particular pattern of infralabial papillae, large flaps behind the nostrils, and parallel, pustulate ridges in

place of the BFA papillae, were observed in no other species. The great difference between *C. nubicola* and *C. subpunctatus*, plus the fact that only two species have been examined, means that it is not possible to provide a single diagnosis for the family Dendrobatidae at this time.

DISCUSSION

FUNCTIONAL CONSIDERATIONS

From structural relationships and knowledge of the habits of various tadpoles, functions can be hypothesized for many of the structures presented in the Descriptions. In the following section variation in internal oral features is reviewed and possible functions for these structures are discussed. In many cases additional comparative and experimental work will be necessary to verify functions proposed here.

KERATINIZED STRUCTURES

Two types of internal keratinized structures have been observed. The first is a medially directed spur located at the posterodorsal corner of the infralabial cartilage, just posterior to the lower beak. These spurs are well developed in *Gastrotheca riobambae* and show weak development in *Agalychnis callidryas* and *Colostethus subpunctatus*. They are too far back in the junction of the jaws to be applied to the substrate and the fact that they are directed medially prevents their occlusion with either the upper or lower beaks. They have not been discussed in the literature, but have been illustrated in *Rana rugulosa* by Noble (1927, Fig. 10). Their occurrence in tadpoles of such diverse morphology, ecology, and relationship makes it difficult to infer a function for these poorly known structures. The spurs simply may be associated with relatively large size in free-swimming tadpoles of certain of the more advanced Type 4 families. It is possible that they

assist in shredding food that is spit in and out of the mouth.

The second type of internal keratinized structure is the median cornified knob in the prenarial arena of *Scaphiopus bombifrons*. This knob has not been described previously, although it was mentioned as a feature that could separate *Spea* from *Scaphiopus* in Altig's "Key to U.S. tadpoles" (1970). The knob is ideally positioned to assist in cutting long, firm plant material. Elongate matter drawn into the mouth would be held in position by the medially directed pair of infralabial papillae. The lower beak would close between the knob and the upper beak, thereby shearing the material. The presence of such a preparative aid to ingestion in *S. bombifrons* is consistent with the known voraciousness of these larvae.

Ueck (1967) reports keratinized structures within the oral tube of a *Hymenochirus boettgeri* larva. Examination of a photomicrograph (Ueck, 1967, Fig. 53), indicates identical morphology with my own sectioned material of this species. What Ueck calls "die verhornten Zellen" appear to be cornified squamous cells in a thickened layer identical to what is seen in the mouth of adult *Hymenochirus* (O. Sokol, pers. comm.). Griffiths (1963) said that the mouth of *Pseudhymenochirus* is "armed" with minute denticles. Although he cited an unpublished observation for proof of this, I find no evidence for such denticles in my own sectioned material of this genus or any other pipid larvae.

INFRALABIAL PAPILLAE

There are normally two major infralabial papillae in all free-swimming tadpoles of Types 3 and 4. These may be augmented by as many as six minor papillae on each side (e.g., *Hyla rufitela*, *Agalychnis callidryas*). The two major infralabial papillae can be long and secondarily papillate (e.g., *Ptychohyla leonhardschultzei*, *Leptobrachium oshanensis*, *Oreolalax*) or short and globose (e.g., *Hyla phlebodes*, *Hyla dendroscarta*).

In *Ascaphus* the individual papillae are replaced by a large, bilobed oral valve (Gradwell 1971a, 1973). This structure can be derived easily from two infralabial papillae that have fused on the midline. This valve allows *Ascaphus* larvae to cling to substrata without continuous pumping. However, such a valve does not occur in other suctional tadpoles (e.g., *Hyla mixe*; see also Gradwell, 1975b, for *Litoria lesueuri*, *L. booroolongensis*, *L. glandulosa*, *L. citropa*, and *Mixophyes balbus*) and is not essential for suctional clinging.

Rhinophrynus has four tiny papillae unlike any seen in other tadpoles.

Judging from the drawings by Weisz (1945), Sterba (1950), Sokol (1962, 1977a) and Ueck (1967), infralabial papillae are absent in the Pipidae.

Microhyla has two or three knob-like infralabial papillae per side.

There are three possible functions for the infralabial papillae: they may function as respiratory structures, sensory structures, or mechanical interactors with food or water currents. Respiration can hardly be a major function of these structures; for even in the species with highly dendritic infralabial papillae, their surface area is only a small fraction of the surface area of the remainder of the buccal floor and pharynx. According to Gradwell (1972a, for *R. catesbeiana*), "Relative to the pharynx and gill cavity the buccal lining is poorly vascularized and is probably of little significance for blood oxygenization by the buccal water currents."

The infralabial papillae extend into the prenasal arena. The common complex, hand-like infralabial papillae are aligned directly in front of the internal nares. In this position the papillae could very easily serve the function of directing particulate matter medially and away from the nares, where large particles could cause obstruction.

A possible function for the simple globose papillae of some species is chemoreception; however, the papillae have a poor surface-to-volume ratio for this purpose. The papillae may be mechanical sensors; in species where they are in medial contact, objects entering the mouth will collide with them. In *Centrolenella*, *Microhyla* and *Megophrys*, the papillae are arranged so that large particles can be prevented from accidentally entering the mouth cavity, a function proposed by Liu (1950, p. 191). Indeed, in funnel-mouthed forms (e.g., *Ptychohyla schmidtorum*, *Megophrys minor*, *Microhyla heymonsi*, *Colostethus nubicola*) the marginal palps fit into the lateral margins of the posteriorly directed "V" of the prenasal arena. A tight tongue-in-groove configuration is formed, making it impossible for large particles to enter the corners of the mouth.

Abundant medium size plant fragments have been observed in the guts of *Hyla microcephala*, which is similar to *Hyla phlebodes* and a close relative of it (Wassersug and Rosenberg, 1979). The globose, medially abutting, infralabial papillae of these species may serve a function of providing information on the position of plant fragments, informing the tadpole when filamentous plant matter is far enough back in the mouth to be bitten off.

The globose infralabial papillae of *Hyla dendroscarta* are an enigma. They may simply be embryonic, considering the early stage of the tadpole examined.

Large, elongate infralabial papillae are seen in all stream-adapted tadpoles that feed on the bottom (e.g., *Ptychohyla*

leonhardschultzei, *Oreolalax*, *Leptobrachium oshanensis*, *Hyla mixe*) except *Ascaphus*. Duellman (1970, p. 412) illustrated large, complex infralabial papillae in *Hyla smaragdina*, a species of the stream-adapted *Hyla sumichrasti* group. The papillae point out of the mouth in these stream forms and may serve as taste or pressure receptors when the tadpoles contact a hard surface. Support for this hypothesis must await experimental or neurohistological studies.

LINGUAL PAPILLAE

Ascaphus has a dense field of several dozen lingual papillae, whereas lingual papillae are absent in microhylids, *Rhinophrynus*, and, by definition, in the aglossal pipids. Discoglossid larvae have a variety of patterns for the surface anatomy of the lingual anlage. At one extreme is *Alytes obstetricans*, with a dense field of pustulations similar to the field of papillae in *Ascaphus*; at the other extreme is *Bombina orientalis* with a single medial projection. *Alytes cisternasii* has two lingual papillae and many pustulations; *Discoglossus pictus* has an arch of six enlarged papillae of which the medial ones are fused. These latter two species demonstrate morphological patterns intermediately between the extremes of the family.

A single medial projection occurs in *Anothea*, but it is grossly dissimilar to that of *Bombina*. Duellman (1970, p. 326) illustrated a single medial projection in *Hyla zeteki*. If this is a homologue to the lingual papilla, it is a remarkable convergence with *Anothea*. (Both *H. zeteki* and *Anothea* are large-mouthed, carnivorous, arboreal larvae.)

The remaining tadpoles examined normally had either zero, two, or four lingual papillae. The papillae were absent in *H. phlebodes*, *H. sarayacuensis*, *H. mixe* and the megophryine pelobatids. In some of these forms, however, anterior papillae or pustulations near the infralabial papillae may be homologues of the lingual papillae. Among the

hylids examined, only *Gastrotheca* has four lingual papillae. *Rana esculenta*, *R. pipiens*, *Pelobates fuscus* and *Bufo cinereus* (= *B. viridis*) have two lingual papillae (Schultze, 1870; Hammerman, 1964), whereas *Rana sylvatica*, *R. catesbeiana* and *R. clamitans* have four (Helff and Mellicker, 1941; Hammerman, 1964). Hammerman (1964) claimed that *R. temporaria* has two lingual papillae, but Savage (1952) illustrates and DeJongh (1968) reports four in this species. Kratochwill (1933) reported four lingual papillae in *Rana agilis* (= *R. dalmatina*). Kenny (1969a) illustrates two lingual papillae in *Phyllomedusa trinitatis*. Lingual papillae have a chemoreceptive function (Hammerman, 1967, 1969; Helff and Mellicker, 1941).

BUCCAL FLOOR ARENA

The BFA is nonexistent in certain species (e.g., *Megophrys minor*, *Hyla phlebodes*, *H. ebraccata*, *H. sarayacuensis*) or ill-defined (e.g., *Scaphiopus bombifrons*, *Centrolenella fleischmanni*) because of the absence of papillae. In all other species studied papillae of the buccal floor define some sort of bilaterally symmetrical area. The arena is usually oval or egg-shaped in the hylids, pelobatids and *Alytes*. Illustrations in the literature indicate that the oval pattern also occurs in *Rana* and *Bufo* (see Savage, 1952). In *Ascaphus*, *Bombina*, *Discoglossus*, *Colostethus*, *Agalychnis* (and its relative *Phyllomedusa trinitatis*, Kenny, 1969a), *Hyla dendroscarta*, and the stream-adapted *Hyla mixe* and *Ptychohyala schmidtorum*, the papillae at the front of the arena diverge to form a "V" or "U" shaped arena. In *Rhinophrynus* and the microhylids the papillae are limited to a broad arc behind the buccal pockets. Papillae of the buccal floor are evidently absent in the Pipidae (Sokol, 1962, 1977a; Ueck, 1967; Sterba, 1950).

The BFA papillae are most often slightly compressed, conical structures,

which if large enough, curve medially. Certain tadpoles have rather specific types of papillae unlike those seen in any other species (e.g., the blunt, out-turned cylindrical papillae of *Anotheca*; the pustulate papillae of *Oreolalax*). The papillae are most numerous and attenuate in the stream species, the extremes being *Ptychohyala leonhardschultzei* (89 papillae) and *Hyla mixe* (70 papillae). Gradwell (1972c) independently noted that papillae of the buccal floor are "better developed" in the stream-adapted tadpoles of *Rana fuscigula* than in larval *R. catesbeiana*.

Bifurcation of BFA papillae seems to be associated with the size of individual papillae rather than with an arena of some specific shape or with the number of papillae. Terminal bifurcations are commonest on the larger papillae in species which have tall papillae.

Possible functions for the BFA papillae are similar to those proposed for the infralabial papillae. Again, respiration may be ruled out as a primary function, although in some of the stream-adapted species the surface of the BFA papillae is substantial. A sensory function is most commonly proposed (Kraetichwill, 1933; Kenny, 1969a and 1969b). Gradwell (1972a) wrote that "the shape and orientation (of these papillae) suggest a role as detectors of particulate material in the respiratory system." While this is plausible, I suspect that the papillae may do more than just sense particles; they could be important both in sorting and directing particulate matter in the mouth. In most species the buccal roof arena and buccal floor arena intermesh; thus, the spaces between the papillae are not large (0.1-1.0 mm on the average). When a particle larger than the distance between two buccal floor or roof papillae comes into the mouth it should be retained medially. Because the arenas narrow posteriorly, particles would then be funneled posteriorly and into the esophagus. Of course, if a particle is so large that it cannot

pass through the BFA and BRA papillae at the back of the arena, it could be coughed out of the mouth. Such coughing motions are well known in tadpoles subjected to irritating substances in the water. One reason for having a buccal straining mechanism is that it prevents large particles from entering the pharyngeal cavity where they might clog the filters or the food traps. A similar sieving function has been proposed by Severtzov (1969).

Stream-adapted tadpoles that scrape food from rocks have the densest mesh of buccal floor and roof papillae. These are tadpoles which ingest a rather coarse, self-generated suspension of foods, as opposed to the free suspension of microscopic plankton found in ponds or pools. The stream tadpoles have reduced gill filters, and instead of using pharyngeal structures to strain their food the major job may be done by the BFA and BRA papillae.

The pond-adapted tadpoles of the *Hyla leucophyllata* and *H. microcephala* groups lack buccal arenas, and must use their small orifices as the primary food sieve. The reduced BFA of *Scaphiopus bombifrons* is difficult to interpret. It is possible that with its relatively fine filter mesh and single large, filter cavity on each side, *Scaphiopus* faces little risk of clogging the filters.

Megophrys minor and, to a lesser extent, *Ptychohyala schmidtorum* and *Colostethus nubicola*, have replaced rows of papillae with ridges. Both of these funnel-mouthed forms have two ridges that extend posteriorly from the tongue anlage and interlock with ridges on the roof of the mouth. These massive structures probably act as baffles, channeling particles backward in the mouth.

BUCCAL POCKETS

The shape and size of the buccal pockets depend on the shape of the posterior margin of the ceratohyals and the anterior margin of the branchial baskets. The pockets may be very large in

all dimensions, as in *Leptobrachium*, or so small as to be nearly absent, as in *Hyla phlebodes*. The pockets are evidently perforated only in *Centrolenella fleischmanni*, *Colostethus nubicola*, *Ptychohyla*, *Similisca sordida*, *Hyla rufitela*, *Gastrotheca riobambae*, *Hyla regilla* (6 out of 9 individuals), *Oreolalax pingii* and *Leptobrachium hasselti*. Some individuals examined were too small to determine the state of this character. Perforation does not seem to be associated consistently with any particular habitat or behavior and is a variable character within genera and species.

The buccal pockets, as folds of skin, allow some autonomous movement of the buccal pump relative to the branchial baskets. One might expect that species with much rotation in the buccal pump (see Wassersug and Hoff, 1979) would have the deepest pockets, but this does not appear to be so.

The significance of perforation of the pockets is not clear. Gradwell and Pasztor (1968) discovered that the buccal pockets were open gill slits in *Rana catesbeiana* and constructed an elaborate hypothesis for the function of "this pharyngeal by-pass." They suggested that the open slits may be a common feature which escaped the notice of earlier workers because of concealment by the posterior walls of the ceratohyals. In a later article Gradwell (1972a) viewed the condition of *Rana catesbeiana* as exceptional, differing from "*Ascaphus*, *Xenopus*, *Scaphiopus*, *Phyllomedusa*, and many other genera." The Australian leptodactylid *Mixophyes balbus* lacks perforated buccal pockets (Gradwell, 1975b). I doubt that the pharyngeal by-pass is of much significance in terms of passage of water. Even in species with large buccal pockets the slits are small compared to the pharyngeal gill openings. Epithelial folds from the walls of the pockets clearly act as valves, retarding passage of fluid. The strange ecological and taxonomic distribution of this character makes it difficult to identify a

function for it. Perhaps perforation is simply an embryonic feature occasionally retained in Type 4 tadpoles.

PREPOCKET PAPILLAE AND OTHER FEATURES OF THE BUCCAL FLOOR

Prepocket papillae, or at least papillae or pustulations over the body of the ceratohyals, are present in virtually all species examined except *Scaphiopus bombifrons*. Typically there are one to three papillae that project backward over the buccal pockets. These papillae are most numerous in species with a "U" or "V" shaped buccal floor arena, where the BFA papillae series becomes continuous with the prepocket papillae series. In species which have few BFA papillae, there are few papillae on the arms of the ceratohyals. *Microhyla*, *Caluella*, and *Glyphoglossus* (see Savage, 1952, Figs. 21 and 26) and, presumably, other microhylids have only one very large prepocket papilla. From the literature one can conclude that such papillae are absent in the pipids.

The prepocket papillae may prevent particles from entering the buccal pockets. Together with the papillae of the buccal arenas they could act as sieves. The lateral roof papillae, in species where they occur, are aligned over the buccal pockets and may assist the prepocket papillae in some protective function. In *Rhinophrynus*, where prepocket and lateral roof papillae are absent, there are transverse ridges on the buccal roof that insert into the buccal pockets; these may accomplish the same protective task.

In many species with numerous buccal floor papillae, a distinctive row or patch of papillae and pustulations may develop behind as well as in front of the buccal pockets. In at least one genus (*viz.*, *Ptychohyla*) these are opposed dorsally by a similar patch. Again, a straining or sieving function may be inferred for these structures.

In species of *Microhyla* there are one or more papillae aligned directly in front

of the glottis. These could be very important in sensing particles entering the mouth and also in directing particles away from the glottis. *Rhinophrynus*, which, like the microhylids, has its glottis arising from the middle of the buccal floor, also has anteromedial papillae in front of the glottis on the buccal floor arena. In *Rhinophrynus*, however, these are paired and lateral to, rather than centered on, the midline.

Other tadpoles have unique arrangements of buccal floor features for which it is not so easy to hypothesize functions. Examples are the transverse row of buccal floor papillae seen in *Hyla rufitela* and the lateral papillate lobes of the tongue anlage in *Leptobrachium oshanensis*. The singular occurrence of these features and our limited knowledge of the ecology and behavior of these tadpoles make functional speculations inappropriate at this time.

VENTRAL VELUM

This is an important valve which separates the anterior buccal cavity from the posterior pharyngeal cavity. Kenny, Gradwell, DeJongh and others have presented evidence to show that the margin of the ventral velum can press against the buccal roof and prevent regurgitation of water from the pharynx when the buccal floor is depressed. The ventral velum also supports the mucosa of the branchial food traps. Only the valvular function of the velum is considered here. Although secretory pits on the dorsoposterior margin of the velum are discussed in this section, comments on the ventral secretory tissue are reserved for the section on the food traps.

Six major configurations of the ventral velum are noted. Two of these have the ventral velum divided into right and left halves and interrupted on the midline. Of these two, one is the condition found in *Rhinophrynus*; the other is the condition in the microhylids (with the technical exception of *Microhyla heymonsii*, see Description and below). In

Rhinophrynus the velum is fully (to its posterior margin) attached to the tops of the filter plates of cb. 2 and 3. In the microhylids it is attached only partially (anteriorly) to the tops of these arches. In both cases major projections of the velar margin are lacking, the margin is gently curved, and the glottis arises from the buccal floor anterior to the velar margin. This condition, which I observed in *Microhyla berdmorei* and *M. ornata*, was observed by Savage (1952, 1955) in *Glyphoglossus molossus*, *Chaperina fusca*, *Calluella guttulata*, *Kaloula pulchra*, and *Hypopachus barberi* (= *aquae*), and by Gradwell (1974) in *Phrynomerus annectens*. Clearly the pattern is typical of the family.

Of the four other configurations for the velum, one is shared by the Orton Type 3 tadpoles, *Ascaphus*, *Bombina*, *Discoglossus* and *Alytes*. This is the condition in which the velum is continuous across the midline, but anchored to the tops of cb. 2 and 3, and the margin is either straight or convex anteriorly between the filter cavities. These four genera are listed here in the order of decreasing thickness of the velar margin.

The most common configuration is for the velum to be continuous across the midline, and partially attached to the tops of the filter rows. Posterior projections of the velar margin are usually present and conspicuous. This is the condition for the dendrobatids, centrolenids, and most hylids examined. Judging from the literature, this pattern is typical of other advanced Type 4 tadpoles. *Scaphiopus bombifrons* and the megophrynines seem to be exceptions. In those tadpoles a fifth configuration is seen. These species have the velum anchored anteriorly but virtually lack any attachment of the velum to the tops of cb. 2 and cb. 3. Schultze (1892) illustrated *Pelobates fuscus* with very tall filter plates on cb. 2 and 3, so it is possible the velum in that species is more like that in the other Orton Type 4 tad-

poles than that in the pelobatids I examined.

The last configuration is the absence of a valvular velum in the pipids (Sokol, 1962, for *Hymenochirus*; Menzies, 1967, for *Pseudhymenochirus*; Weisz, 1945; Sterba, 1950; and Gradwell, 1971a, for *Xenopus*; Sokol, 1977a, for *Pipa*). Not all pipids are identical. In *Xenopus* the floor of the common pharyngeobranchial tract is covered by secretory ridges morphologically similar and presumably homologous (Kenny, 1969b) to those found on the ventral surface of the ventral velum in Type 4 tadpoles. In *Hymenochirus* and *Pseudhymenochirus* the surface is devoid of any organized secretory tissue.

In species with a valvular velum there is always positive pressure in the atrial chamber surrounding the gill filaments and one-way flow out of the spiracle. The division of the ventral velum into right and left halves in *Rhinophrynus* and the microhylids should not affect the valvular function of the velum. Even for species with an undivided velum, Kratochwill (1933) and Kenny (1969a) argued that the flow of water from the buccal cavity into the pharynx will be by separate right and left streams. Gradwell (1970) verified this and showed experimentally that each side of the velum can act independently in *R. catesbeiana*. This independence is obligatory in *Rhinophrynus* and the microhylids. In the pipids, which lack a valvular velum, one-way flow is achieved by the opercular flaps acting like valves, opening and closing with each cyclic depression of the buccal floor. For these species atrial pressures must be lower than ambient pressures during part of the cycle.

For any species the mobility of the velar margin and the strength of the valvular seal are determined by the velar length and thickness, the extent of attachment of the velum to the underlying filter plate, and the stiffness and length of the spicules. In most species the

velum can close passively from back pressure. This is the same mechanism that closes similarly shaped pocket valves in the vertebrate circulatory system. Because of the long attachment of the velum to the tops of the filter plates in *Ascaphus*, discoglossids and *Rhinophrynus*, not only the velum but the posterior portion of the hypobranchial plate must rotate upward in order for the buccal floor to be sealed off from the filter chambers. In all tadpoles except pipids (Sokol, 1977a) the anterior edges of the hypobranchial plates are overlapped by the ceratohyals. As the ceratohyals are depressed the hypobranchial plate rotates on a transverse axis. This mechanism aids in closing the velar valve and is reviewed in Wassersug and Hoff (1979). (As a functional complex, this mechanism provides insight into why pipids, which lack the hypobranchial/ceratohyal articulation, also lack a valvular velum.)

In *Ascaphus truei* there is a posteriorly directed "V"-shaped trench on the buccal roof above the ventral velar margin. The thickened velar margin insets into the trench when the valve is shut. Such a structural arrangement is reminiscent of a gasket on a high pressure seal. That such a system should appear in this torrent-adapted larva is no surprise. Gradwell (1971a) found a mean maximum oral disc suction of -125 torr in five live, stage 32 *Ascaphus* tadpoles.

The discoglossids show a thickened velar margin similar to that of *Ascaphus* but not as extensive. They also lack a trench on their buccal roof.

Although *Rhinophrynus* has little mobility of the velar margin, the roof of the mouth above the free velar surface is contoured to assure sufficiently large contact area to close the valve.

All the stream tadpoles with suctorial mouths except *Ascaphus* have spicules that are longer, stouter, or both, than the spicules of *Hyla regilla* or *Acris crepitans*. These stream forms must produce relatively great negative buccal pressures

in order to adhere to rocks with their oral discs. Presumably, the enlarged spicules serve to strengthen the valve and prevent prolapse. The tadpoles of the *Hyla leucophyllata* species group have wide spicules and a thickened free velar surface. One can hypothesize that these tadpoles produce relatively great suction during inspiration. This may be important for drawing rather large fragments into the mouth. *Hyla phlebodes* has a very short ventral velum unsupported by spicules. The shortness of the velum insures some protection from collapse when the valve is elevated. *Microhyla heymonsi*, which appears to feed on large particles, has the thickest and presumably the strongest ventral velum in the genus. *Microhyla berdmorei* and *M. ornata*, in contrast, have very delicate ventral vela and it is clear that they could not endure a high pressure differential between the buccal and pharyngeal cavities without a collapse of the valve.

Two arboreal species, *Hyla dendroscarta* and *Anothea spinosa*, have reduced ventral vela with little or no spicular support. The velum may be a functional valve in *H. dendroscarta*, but is so reduced in *A. spinosa* that it is hard to imagine how it could function. In *Anothea* the pharyngeal cavity itself is also extremely reduced, so that it may not matter whether the velum is valvular or not. The most unusual vela were seen in *Megophrys minor* and *Scaphiopus bombifrons*. At the present, the functional implications of their velar shapes are obscure.

Two general patterns are evident for sculpturing of the velar margins as seen in dorsal view. This edge is most likely to appear as a smooth, gentle arc in tadpoles associated with standing water. In tadpoles associated with moving water marginal projections are distinct and numerous along the velar margin. There are, however, some outstanding exceptions. Marginal projections are lacking in *Ascaaphus* and quite distinctive in

Agalychnis. When present, projections usually number one each for each filter cavity, with two or more additional projections in front of the esophagus. Supernumerary projections are present in *Leptobrachium* and *Oreolalax*. In these, general projections may arise from the ventral medial surface of the velum as well as from the posterior medial edge. The most extreme development of supernumerary projections is seen in *Leptobrachium oshanensis*, which has a multi-layered papillate fringe on the medial edge of its ventral velum. When the branchial baskets are an unusual shape, such as with the reduction of filter cavity 3 in certain stream tadpoles, there is a concomitant shift in the position of the projections (medial in the example of the stream tadpoles; see below).

There is no literature concerning the possible function of the velar projections, although they must affect the valvular workings of the velum. With long and numerous projections such as are present in stream tadpoles, it becomes impossible for the velar seal to open or close abruptly. The projections may play a role in regulating laminar flow and directing currents over the edge of the velum when the buccal floor is elevated and water is pushed over the velar edge into the pharynx.

The medial portion of the ventral velum is displaced dorsally and anteriorly in *Anothea* and *Gastrothea* due to a large laryngeal disc. The same portion of the velum is turned upward and forward in *Ptychohyla schmidtorum* and *Leptobrachium oshanensis*, but neither of these species has a large, early developing glottis. Although the configuration in these two species may be a preservational artifact, it is strange that it should occur in larvae of such similar overall ecology.

In a general way, the extent of development of the median notch reflects the size and development of the glottis. At one extreme is *Anothea spinosa* with a median notch half the width of the

ventral velum and a large, functional glottis, which develops early, exposed within. At the other extreme is *Ascaphus truei*, which lacks a median notch and functional lungs as a larva.

The secretory pits on the velar margin have been discussed previously by Kenny (1969b) for one species (*Pseudis paradoxa*) and more recently and extensively for a large variety of species by Wassersug and Rosenberg (1979). No particular pattern of density or size is evident other than that the pits are most common on the posterior projections of the velar margin and consequently most numerous in species with well developed posterior velar projections. In *Ascaphus* and *Bombina* a fine-grained secretory tissue is seen under the dissecting microscope instead of well organized secretory pits. In *Alytes* a few tiny pits can be seen on the margin, while in *Rhinophrynus* secretory pits *per se* are absent from this region. In species with a reduced velum (e.g., *Hyla phlebodes*) secretory tissue along the ventral velar margin cannot be resolved with light or scanning electron microscope (Wassersug and Rosenberg, 1979).

The pits of the ventral velum oppose the secretory tissue of the glandular zone and presumably function in concert with that tissue. As noted by Kratochwill (1933), the edge of the free velar surface matches the shape of the glandular zone. Gradwell (1970) suggested that friction of the velar edge meeting the buccal roof may be reduced by mucous secretion. This mucus could be extruded from the margin of the ventral velum as well as the glandular zone and, as discussed by Wassersug and Rosenberg, could act both to lubricate and seal the valve. Kenny (1969b) and Wassersug and Rosenberg (1979) have suggested that the secretory pits may be involved in the food trapping process. Mucous strands excreted by the secretory pits of the roof and floor could catch and aggregate plankton much as

has been proposed for the mucous strand generated by the secretory ridges under the velum (Wassersug, 1972).

THE FILTER SYSTEM

Different species vary enormously in the extent of the development of the filters. This variation is most evident in the size and shape of the branchial baskets. Massive branchial baskets characterize *Agalychnis callidryas*, *Phyllomedusa trinitatis* (Kenny, 1969a), the microhylids excluding *Microhyla heymonsi* (see Savage, 1952, 1955, for genera other than *Microhyla*), *Xenopus* (Sterba, 1950; Ueck, 1967) and free-swimming *Pipa* (Sokol, 1977a). Among the species examined, *Bombina orientalis*, *Scaphiopus bombifrons*, *Hyla femoralis*, *Hyla rufitela*, and *Gastrotheca riobambae* have baskets slightly larger than "typical" pond larvae, such as *Hyla regilla* and *Acris crepitans*, but not nearly as large as in the species just mentioned. In those species with an enlarged pharynx the greatest increase in size is in the length of the filter plate. Also commonly exhibited is an increase in height. The ceratobranchials tend to have a more longitudinal, less oblique, orientation in these forms. *Scaphiopus* is somewhat an exception in that its branchial baskets are bowl-shaped and, although larger overall than those of *H. regilla*, the filter plates of cb. 2 and 3 are much reduced in height.

Large branchial baskets are associated with specialization for suspension-feeding, particularly in species which lack keratinized mouth parts (Savage, 1952). However, one must be cautious of this generalization (see Kenny, 1969a); pharyngeal size alone cannot be the determining factor for the size range or volume of particles removed from the water by a tadpole. The density of the filter mesh, and other oral features such as buccal floor and roof papillae, branchial food traps (Wassersug and Rosenberg, 1979), volume of the buccal pump (Wassersug and Hoff, 1979) and

size of the orifice will have a profound effect on the quality and quantity, including size range, of food ingested.

At the other extreme, the filter baskets are much reduced in *Hyla phlebodes* and *Anotheca spinosa*, and slightly reduced in *Hyla sarayacuensis*, *Colostethus nubicola*, *Microhyla heymonsi* and *Megophrys minor*. Filter surfaces are totally lacking in *Hymenochirus* (Sokol, 1962; Ueck, 1967) and in *Pseudhymenochirus* (pers. obs.). Reduction is exhibited in both the height and length of the filter plates.

Reduction of the branchial baskets occurs in three types of tadpoles. The first includes known carnivores such as *Hymenochirus* and *Anotheca*. These tadpoles lack any ability to extract fine plankton from suspension and instead select relatively large individual prey items. From stomach contents (Parker, 1931; Cei, 1968) it would seem that the aberrant leptodactylid *Lepidobatrachus* fits into this class; indeed, serial sections of *Lepidobatrachus llanensis* larvae reveal extreme reduction of the branchial baskets (Wassersug, unpublished).

The second type includes tadpoles which feed at the surface using upturned funnel mouths. Examples are *Colostethus nubicola*, *Microhyla heymonsi* and *Megophrys minor*. This reduction suggests that funnel-mouthed tadpoles are not as dependent on microscopic particles for food as is implied by some of the older literature. Pope (1931) commented on the sparsity of microscopic organisms in the clear mountain pools inhabited by funnel-mouthed larvae. Heyer (1973) found small arthropods in the guts of larval *M. heymonsi*, and Smith (1917) showed surprise at the relatively large particles that *Microhyla achatina* could ingest.

The last type of tadpole with reduced branchial baskets includes pond species which lack denticle rows, exemplified by *Hyla phlebodes* and, to a lesser extent, by *Hyla sarayacuensis*. Wassersug (1973) suggested that hyloid larvae with fila-

mentous tails and reduced denticle rows may be convergent with truly specialized suspension-feeders such as *Xenopus*, but this now appears to be an overgeneralization, at least for *H. phlebodes*. In an earlier part of this discussion, it was suggested that *H. phlebodes* tadpoles may ingest vegetative strands that they cut into fragments of moderate size. The reduction of the branchial baskets is consistent with the view that larger fragments and not the smaller plankton are the important food for this species. Larvae of the ranid genus *Ooeidozyga* have mouths which are similar in gross features to the hyliids of the *H. leucophyllata* and *H. microcephala* species groups. Serial sections of the pharynx and digestive tract of an *Ooeidozyga laevis* larva reveal reduced branchial baskets as well as coarse plant matter in the intestines (Wassersug, unpublished). While this further demonstrates convergence with certain hyloid larvae, the observation does not support the view that *Ooeidozyga* larvae are carnivorous (Alcala, 1962). Heyer concluded from his study of larval gut contents that *Ooeidozyga* tadpoles are omnivores, or if carnivorous, only facultatively so.

Stream-adapted tadpoles do not show any strong trend toward either expanded or reduced branchial baskets. However, a common feature of bottom-dwelling forms with suctorial mouths is an anterolateral displacement of the posteromedial edge of the branchial baskets. This gives the third filter cavity a truncated appearance. Also, there is a tendency (except in the stream megophrynines) toward extensive imbrication of the filter plates. These modifications, amounting to a broadening and dorsal-ventral shortening of the pharynx, are consistent with the low, broad, profile characteristic of stream-adapted organisms (Hora, 1930). *Centrolenella* larvae, in contrast, exhibit elongation of the filter cavity. Their branchial profile appears to reflect the general elongation of

the tadpole and can be understood as an adaptation to burrowing (Gans, 1975).

Although relative size only is discussed above (i.e. size of the pharynx compared to size of the buccal cavity), it should be noted that there seems to be a natural upper limit on the absolute size of the branchial baskets. Despite their giantism, larvae of *Pseudis paradoxa* have branchial baskets no larger than those of bullfrog tadpoles one third to one half their total length (Parker, 1881).

Directly correlated with the overall size and shape of the branchial baskets is the number of filter rows on each filter plate. The number of filter rows, however, is somewhat affected by the absolute size of the pharynx, so comparison of species with very large larvae with species with very small larvae may give slightly different counts even though the tadpoles have the same shape and proportions.

Of the species examined, the highest counts for filter rows were in *Microhyla berdmorei*, *M. ornata*, *Rhinophrynus dorsalis* and *Agalychnis callidryas*, whereas the lowest counts were in *Anotheca spinosa* and *Hyla phlebodes*. In the above species, counts were significantly ($p < .05$) different from *Hyla regilla* for all four filter plates (cf. Table 1; Wassersug, 1976b). In certain other species, one or two, rather than all four, filter plates had significantly fewer or more filter rows than *H. regilla*. Thus, *Hyla sarayacuensis* shows a tendency toward reducing the number of filter rows as does *Leptobrachium hasselti*, whereas *Scaphiopus bombifrons* and *Hyla femoralis* show a tendency toward increasing the number of rows.

Kratochwill (1933) gave counts for filter rows in *Rana dalmatina* that were within the range for *Hyla regilla*, except for cb. 4, which had a higher count. Such a difference may reflect differences in the shape of the branchial baskets or in counting procedure. There are no filter rows to count in *Hymenochirus* (Sokol,

1962), whereas *Pipa carvalhoi* has counts of approximately 14, 19, 25 and 16 (Sokol, pers. comm.), all significantly above the range for *H. regilla*. From Sterba's (1950) illustration it is clear that *Xenopus laevis* has significantly more filter rows on all arches than does *H. regilla*. The number of filter rows seems like a rough, but good, indicator of the amount of effort any species puts into microphagous suspension feeding.

Substantial variations in the filter mesh between species provide a clear indication of a species' ability to extract small particles from suspension. Filter porosity, however, may not be the absolute determinant of the lower size limit of the particles a filter feeder can extract (Kenny, 1969a; Wassersug, 1972; see LaBarbera, 1978). Of the species examined, *Rhinophrynus dorsalis*, *Agalychnis callidryas*, *Microhyla berdmorei*, and *M. ornata* have a particularly tight filter mesh, whereas *Anotheca* and *Hyla phlebodes* have no filter mesh. Species with a filter mesh slightly denser than that of *Hyla regilla* include *Hyla femoralis*, *Hyla rufitela* and *Gastrotheca riobambae*. Species with a slightly less dense mesh are *Ascapheus truei*, the discoglossids, megophryne pelobatids, dendrobatids, *Microhyla heymonsi*, and the remaining hylids with the exception of *Acris crepitans* and *Smilisca sordida*. *Scaphiopus bombifrons* has a denser filter mesh than *H. regilla* on the rows proper but greater spaces between the rows.

A tight filter mesh is most commonly achieved by longer tertiary branches on the filter folds and by an increase in the number of higher order folds. It is possible to achieve a tighter mesh without changes in the branching pattern by widening the individual side folds (e.g., *Agalychnis*) or by widening the rows *in toto* (e.g. *Gastrotheca*). The continuation of filter rows from one filter plate to the next over the gill slits at the bottom of the filter cavities is a unique feature of *Gastrotheca*. This assures that large

particulate matter in the filter cavities cannot accidentally escape through the gill slits into the atrial chamber. Sokol (1977a) reports a somewhat similar situation in free-swimming *Pipa* larvae. In these tadpoles, however, filter ruffles are fused with the ruffles on neighboring rows of each filter plate rather than vertically over the gill slit. In *Pipa*, filter canals are present but overlaid with a continuous filter mesh that must be cut in order to expose the canals. I have verified this unusual anatomy in my own material of *Pipa parva*.

Reduction of filter mesh is most commonly achieved by deletion of higher order folds and shortening of secondary folds. Slight reduction can be accomplished without a change in the branching pattern by a simple thinning of all the folds. Wispy ribbons of tissue remain as the vestiges of filter rows in *Anotheca spinosa*. In the extreme reduction of the filter rows of *Hyla phlebodes* the main fold is retained as a raised knob on the gill bar.

A few species have filter rows that are distinctive for other reasons than the tightness of their filter mesh. *Ascaphus truei* and *Bombina orientalis* share unusually straight main filter folds with short, robust, side branches.

Kenny (1969a) labelled the tops of the filter folds as filter ridges in *Phyllomedusa trinitatis* and called the edges of the filter ridges "filter shelves." However, Gradwell (1972a) states that he found no filter shelves or filter crevices in *Rana catesbeiana*, whereas he does identify "pointed cells" at the crests of the ridges. I suspect that the discrepancy observed here is more the result of semantics and preservational artifacts than true differences between species. Both Kenny's and Gradwell's Fig. 9—their independent illustrations of the filter rows—are somewhat ambiguous. I interpret the "tops of the filter ridges" of Kenny to be the same as the "pointed cells" of Gradwell. Under this designation, *Rana catesbeiana* must necessarily

have filter shelves. The acuteness of the ridge tips will vary with preservation. Gradwell preserved his specimens in Bouin's Reagent, which tends to shrink tadpoles more than preservatives used by Kenny. Shrinkage would accentuate the ridge tips, narrow the filter shelves, and open the filter niches in such a way that individual filter crevices may not be obvious.

Gradwell (1972a) has discussed the filters as respiratory structures. They are well vascularized, but their actual importance to gas exchange has not been measured and must vary greatly between species. In tadpoles such as *Xenopus* which lack gill filaments, the gill filters are obviously important respiratory structures (Millard, 1943).

In many of the specimens examined, flocculent matter covers the filter surfaces or packs the anterior ends of the filter cavities. There can be little question that the main function of the filters is to retain in the pharyngeal cavity particulate material which enters the mouth with the respiratory current. The current discussion is limited to a consideration of the role of the filters in feeding.

Kenny (1969a) set the lower limit for the dimensions of the filter niches at 5 μm for *Phyllomedusa trinitatis*. Because *P. trinitatis* has large, dense filters, this may be near the lower limit of the pore size for anurans in general. This measurement of 5 μm , however, was made on fixed material and, as noted by Kratochwill (1933), under positive pharyngeal pressure the filters should flatten and expand to form a tighter mesh. The strange, truncated shape of the filters and their resilience may relate to this ability to vary surface area and porosity with pressure. Under actual feeding conditions the filter niches may be smaller than 5 μm in some of the species specialized for suspension-feeding. Nevertheless, when very fine particulate matter is found on filter surfaces, the particles are invariably clumped in mucus; yet the filters themselves are not

secretory. Thus, despite fluctuating filter niche porosity, ultraplanktonic entrapment must be initiated elsewhere in the mouth than on the filter surfaces.

Questions remain as to how food matter is removed from the filter, and why mucus does not adhere more tenaciously to these surfaces. Kenny (1969a) has suggested that there is some backwash through the filters during part of every pumping cycle. In *Rana catesbeiana*, however, the pharyngeal pressure is only briefly and very slightly negative during the pumping cycle (Gradwell, 1972b), so that backwashing is unlikely. Reorientation of the filter plates may actually dislodge food particles from the filter plates during each pumping stroke. Because of rotation in the hypobranchial plate the filter plates should be stretched every time the buccal floor is depressed. In most species, the pressure cushions are shaped to fit the filter cavities closely. The secretory pits found on the cushions might help lift material from the filters. The answer to why mucus does not clog the filters could conceivably lie in some aspect of the histochemistry of the mucus and the cells that make up the filter epithelium. Kenny (1969b) noted that the cells which line the filter niches can be distinguished from other cells in the filters because they stain unusually heavily with Orange G.

BRANCHIAL FOOD TRAPS AND SECRETORY RIDGES

In most species the entire free velar surface is covered ventrally by secretory ridges. Thus, the parameter most relevant to the size of the branchial food traps is the size of the free velar surface. The height of the branchial baskets may also affect the size of the collecting surface because the secretory ridges commonly cover a portion of the anterior and lateral surfaces of the filter plate. When the branchial baskets are very shallow, the ventral extent of the secretory area must be limited. Of the spe-

cies examined, the largest collecting surfaces were observed in *Gastrotheca ribambae* and *Agalychnis callidryas*. The smallest were seen in *Hyla phlebodes*. Branchial food traps are absent in *Anotheca* and we may conclude from the literature that they are absent in *Hymenochirus* and *Pseudhymenochirus* (Sokol, 1977a).

The shape of the area covered by secretory tissue is largely determined by the shape of the ventral velum. Where the velum is completely anchored to the top of the filter plate (in *Ascaphidae*, *Discoglossidae*, and *Rhinophrynidae*), each filter cavity has a separate collecting area. In *Ascaphus* and the discoglossids the branchial food traps are further distinguished by a large, elevated rim that separates them ventrally from the filter surfaces on the filter plates. *Leptobrachium* has an expansion of the area covered by secretory tissue onto the dorsally facing surface between the fourth ceratobranchials anterior to the glottis.

The microhyids and *Rhinophrynus* have collecting surfaces which are similar in their gross shape. The surface is more (e.g., *Microhyla berdmorei* or less (e.g., *Microhyla heymonsi*), restricted to a dense, narrow, vertical crescent at the anterior end of the filter cavity. In *Microhyla berdmorei* much of the velar surface is devoid of secretory tissue.

Perhaps the most unusual collecting surfaces occur in *Xenopus*. Here the secretory ridges are transposed to the ventral surface of the common buccopharyngeal cavity along the top of the filter plates. The gross shape of this secretory surface has been described and illustrated by Weisz (1945), Sterba (1950), Gradwell (1971a, 1975a) and Sokol (1977a). *Pipa* and *Hymenochirus* lack these collecting surfaces (Sokol, 1975).

The histology of the secretory tissue has received extensive discussion by Kenny (1969b) and Wassersug and Rosenberg (1979). Kenny reported secretory pits in *Pseudis paradoxa* along

the margin of the ventral velum and thought them unique to *P. paradoxa*. Secretory pits are in fact common on the most posterior edge of the velum in many species, particularly those with long velar projections. Organized secretory ridges (Wassersug, 1972) are absent in the Ascaphidae, Discoglossidae and Pelobatidae. In these forms the collecting surfaces have a fine-grained texture under light microscopy, indicating the presence of secretory cells but without the ridge organization. *Rhinophrynus* shows some development of ridges on part of the branchial food trap surface. Secretory ridges degenerate in *Hyla regilla* near metamorphic climax.

Kenny (1969b) found no evidence that secretory cells were arranged either in pits or rows in the tadpoles of the hylid *Amphodus auratus*. *Amphodus* larvae are arboreal, and Kenny associated the absence of a ridged pattern with the unusual larval habitat of this species. I could not perceive secretory tissue under the velum in either *Anotheca spinosa* or *Hyla phlebodes*, nor could I find any ridges in *Hyla dendroscarta*. In members of the *Hyla leucophyllata* group, secretory ridges appear concentrated in the more anterolateral region of the pharynx near the ciliary groove. Whereas the above tadpoles are a rather heterogeneous assemblage, they do offer some support for the idea that absence of secretory tissue in tadpoles of advanced frogs is associated with abandonment of microphagous suspension-feeding as the sole source of nourishment.

The amplitude and frequency of secretory ridges may be important in determining the potential of the secretory surface to trap particles of a particular size or density. The pattern of the ridges seen in *Xenopus* (Kenny, 1969b) is unique for that genus. The ridged pattern in the microhylids is also unique for that family. In a general way, Kenny associates the features of the ridges in *Xenopus* and the microhylids with a specialized, suspension-feeding way of life.

Although I have concurred with this view (Wassersug, 1972), the question of the functional meaning of the textural patterns of secretory tissue remains unanswered.

GLOTTIS AND LARYNGEAL DISC

There seems to be considerable range in the size of the glottis and laryngeal discs, although most species do not vary much from the proportions observed in *Hyla regilla*. The extremes were seen in the discoglossids, *Anotheca* and *Hyla phlebodes* at the upper limit and *Ascaphus truei* at the lower. To some extent an enlarged glottis seems to characterize large individuals. A large glottis is clearly associated with early functioning of the lungs for respiration or hydrostasis. The small glottis seen in larval *Ascaphus truei* is consistent with the fact that these tadpoles live in well-oxygenated water where stability in a current could be jeopardized by air-filled lungs. Although *Ascaphus truei* is the extreme, other stream-bottom forms also show some reduction in the size of the glottis compared with typical pond larvae. *Bufo* larvae which have a small nonfunctional glottis develop their lungs just before metamorphosis (Savage, 1950 and 1961; Starrett, 1973) and it is no surprise that they are relatively restricted to a bottom habitat in water of low turbidity (Wassersug, 1973; see also Wassersug and Seibert, 1975).

The position of the glottis in relation to the velar margin again reflects larval lung utilization. *Rhinophrynus*, microhylid, and pipid larvae all have the glottis fully exposed on the buccal floor. These are tadpoles which have the ability to stay in the water column continuously, and their lungs must have a hydrostatic function. Although the remaining tadpoles have the glottis behind the ventral velum, many have it fully or nearly fully exposed when viewed from above. These include the larvae of *Scaphiopus bombifrons*, *Leptobrachium oshanensis*, *Hyla phlebodes*, *Hyla den-*

droscarta, and *Colostethus subpunctatus*. On the other hand, the nonfunctional glottis of *Ascaphus* tadpoles is fully blanketed by the ventral velar margin. Evidently, accessibility to the glottis may be associated with early function of the lungs for respiratory as well as hydrostatic regulation.

ESOPHAGEAL FUNNEL

The lumen of the esophageal funnel will limit the size of the largest food item that can enter the alimentary canal. In this regard the data in the descriptions, although subjective and only comparative, are valuable as one index of feeding potential. Ueck (1967) noted a great discrepancy between the sizes of the esophagus in *Xenopus* and *Hymenochirus*. *Xenopus* has a strictly microphagous diet and consequently a slender esophagus. *Hymenochirus* is strictly a carnivore on large prey; it has a comparatively huge esophagus.

Among the tadpoles examined, the largest esophageal bore is seen in *Anotheca* larvae. The discoglossids, *Hyla phlebodes*, *H. ebraccata*, *H. sarayacuensis*, and the funnel-mouthed microhylids, all have relatively large esophagi, suggesting an ability to ingest comparatively large particles. The non funnel-mouthed microhylid larvae have esophagi with the smallest diameter. This observation is consistent with the view that these tadpoles are specialized for microphagy.

The profile of the esophageal funnel reflects the shape of the posterior margin of the branchial baskets. Because of the lateral displacement of the third filter cavity in tadpoles associated with the stream habitat (with the exception of *Ascaphus truei*), these forms tend to have broad esophageal funnels. Distinctly broad esophageal funnels can also be seen in the discoglossids, certain dendrobatids (*Colostethus subpunctatus*), amphignathodontine hyliids, and the *Hyla microcephala* and *H. leucophyllata* species groups. A conspicuously narrow

lumen characterizes the non funnel-mouthed microhylids and *Agalychnis callidryas*. The narrow esophageal funnel in the larvae of these species is ascribable to the relatively elongate branchial baskets that bound the esophagus.

PRENARIAL ARENA

For any tadpole, the size and shape of the prenarial arena is determined by the position of the internal nares, the breadth of the upper beak, and the curvature of the rostrum. The nares are far forward in *Rhinophrynus* tadpoles and larvae of the *Hyla microcephala* and *Hyla leucophyllata* species groups; consequently, these species have small prenarial arenas. Another larva with a greatly reduced prenarial arena is *Ascaphus truei*; this is also the species with the strongest posteroventral curvature of the rostrum. Wide prenarial arenas characterize the amphignathodontine hyliids, microhylids, and funnel-mouthed tadpoles in general, although a comparatively narrow prenarial region is found in the megophrynine pelobatids, excluding *Megophrys*.

Many species have specific structures within the prenarial arena. The functional significance of only a few of these are comprehensible given the sample at hand. A distinct, posteriorly directed "V" shaped ridge occurs in *Ptychohyla schmidtorum*, *Megophrys minor*, *Colostethus nubicola* and *Microhyla heymonsi*, but in no other species examined. The ridges interlock with a palp-like infralabial papillae in these funnel-mouthed forms and, as has been suggested earlier, could prevent large particles from entering the corners of the mouth. We may expect to find this structural arrangement in other funnel-mouthed species.

The huge, fleshy, pustulate cone descending from the prenarial arena in *Hyla mixe* is of sufficient size to occlude the oral opening. In the absence of an oral valve derived from the infralabial papillae (cf. *Ascaphus*), this dorsal

structure may serve a valvular function.

A pustulate or papillate, anteriorly curved crest is present in the prenarial arena of *Hyla femoralis*, *Colostethus subpunctatus*, *Ptychohyla leonhardschultzei*, *Agalychnis callidryas*, *Anotheca spinosa*, and *Smilisca sordida*. This is a group of larvae of such ecological and taxonomic diversity that a single function may be unlikely for this crest. *Centrolenella fleischmanni* has a short transverse ridge in the prenarial area; several other tadpoles have single, knob-like structures in this region (e.g. *Hyla rufitela*). Comparing pictures of the dorsal and ventral surfaces of the various tadpoles shows that all these structures lie immediately above and behind the lower beak when the mouth is closed. They may have a mechanical function related to maintaining beak occlusion or positioning and anchoring macroscopic food items during mastication. Alternatively, future histological work may reveal that this prenarial feature serves a sensory role. Orton Type 1, 2 and 3 larvae lack these structures.

The keratinized knob in the prenarial arena of *Scaphiopus bombifrons* has been discussed already under the heading Keratinized Structures.

INTERNAL NARES

The nares are perforated in all but microhylid tadpoles. They may be large open vacuities, as in *Centrolenella* and the discoglossids, or diminutive structures, as in *Hyla phlebodes* and *Rhinophrynus*. When the nares are larger than in typical pond larvae, such as *Hyla regilla*, they also tend to be more elongate and more obliquely oriented. A few species have internal nares more transversely oriented than *H. regilla*; these include the megophryine pelobatids, *Rhinophrynus*, the dendrobatids, and *Ptychohyla schmidtorum*. In the elongate *Centrolenella fleischmanni* tadpoles the nares are, understandably, longitudinally oriented.

The fact that the nares do not per-

forate until late in development in the microhylids may relate to the efficiency of their buccal pump. Presumably, the risk of leakage at a valve is reduced with fewer orifices that open and close with each pumping cycle.

In nonmicrohylid larvae the anterior narial walls are commonly thickened and pustulate, with one or two small, prenarial papillae. While it is possible that such prenarial projections are sensory, their position directly in front of or under the narial openings suggests that at least the larger papillae serve a protective function. They could keep larger particles from moving up into the nares, where they might disrupt valvular action or might detrimentally coat olfactory surfaces. In species where general oral papillation is reduced, pustulations or papillae of the narial walls are invariably absent. On the other hand, proliferation of floor and roof papillae does not necessarily mean an increase in the number or size of prenarial papillae.

Megophryine pelobatids tend to have a short ridge projecting forward from the anteromedial edge of the narial wall into the prenarial arena. In approximately the same region anterior to the nares, *Hyla rufitela* and *Centrolenella fleischmanni* develop a large *cul de sac* not of the same shape but presumably having the same chemoreceptive function. *Ascaphus truei* has somewhat similar, but smaller and more lateral, pits adjoining the anterolateral wall on each side. The "ciliated epithelial bands" reported in this region by Van Eeden (1951) may be important in cleansing these organs. *Leptobrachium* and *Oreolalax* have the most attenuate prenarial papillae of any of the tadpoles examined; however, the most extreme modification of anteronarial walls are the flaps found in the discoglossids. These flaps are most likely protective. The fact that they should develop in the discoglossids and no other taxa may be related to the plane of the buccal floor and roof in

discoglossids compared to other families. Discoglossids have a buccal floor that tips gently downward anterior to the pharynx and they lack a strong rostral curvature. Most other species examined have a comparatively horizontal buccal cavity and abrupt curvature in the rostral region. With this latter orientation feeding currents impinge on the pre-narial arena before being deflected backward. In the discoglossids, however, feeding currents must flow into the mouth along a more posteriorly directed course toward the internal nares. If not for the flaps on the anterior narial walls, olfactory tissues could be abraded by coarse particles in the feeding currents.

The posterior walls of the nares are sufficiently flexible and properly positioned to act as valves in all the tadpoles examined except the microhylids and possibly the arboreal hylids. The dimensions of the valves strictly reflect the dimensions of the nares. The narial valve projections, however, vary substantially in size. In approximately half the species examined (megophryine pelobatids, microhylids, *Hyla rufitela*, *H. femoralis*, *H. dendroscarta*, *Anotheca spinosa*, *Gastrotheca riobambae*, *Agalychnis callidryas*, and *Acris crepitans*) have narial valve projections equal to or larger than those of *H. regilla*. Dendrobatids have smaller valve projections. Of the remaining forms many, such as all Orton Type 1 and 3 larvae, *Centrolenella*, *Hyla phlebodes*, *H. ebraccata*, and *H. sarayacuensis* tadpoles, lack the projections. The narial valve projections of *Anotheca spinosa* are in the middle of the posterior walls on each side rather than at the medial corners. The most attenuate narial valve projections occur in *Leptobrachium* and *Oreolalax* larvae. Although narial valve projections may be sensory structures, it is equally likely that, in conjunction with pre-narial papillae and pustulations, they block large particles from entering the internal nares.

In the microhylids that I examined

the narial valves are abbreviated transversely but expanded forward and downward as large, cup-shaped projections. Judging from the diagram of Savage (1952, 1961), and Gradwell (1974), this is typical of the family. These projections are stiffened by a ridge that runs down their posterior margin. Noble (1927) illustrates these projections in *Microhyla pulchra*, noting that they would effectively isolate the olfactory chambers from the buccal cavity on each side. He also speculates that these flaps could control and even direct water into the higher portions of the olfactory chambers. Gradwell offered the same hypothesis for the function of these structures in *Phrynomerus*; it seems like a very reasonable hypothesis.

POSTNARIAL ARENA

Superposed photographic prints and drawings of the floor and the roof of the mouth reveal that the tongue anlage makes a near-perfect fit into the post-narial arena. Species which have a poorly outlined postnarial arena (e.g., microhylids, *Rhinophrynus*, *Hyla phlebodes*, *H. ebraccata*, and *H. sarayacuensis*) also tend to show little development of the tongue during the stages that I examined. Similarly, it is reasonable that postnarial arena structures are absent in the aglossal pipids. Other than to form a receptacle for the growing tongue, the roles of the postnarial papillae and median ridge are not evident. Although they have been variously illustrated (Goette, 1874; Schulze, 1889; Kenny, 1969a and 1969b), and DeJongh (1968) offered a fairly complete description for *Rana temporaria*, no author has discussed these or any of the other buccal roof structures in a systematic fashion. Except for Kenny (1969a and 1969b), who labelled these projections along with the lateral ridge papillae as "sensory," no function has ever been suggested for them.

When a postnarial arena is present, it is bound laterally by an average of 2

or 3 postnarial papillae and assorted pustulations. The greatest number of postnarial papillae that I counted in any specimen was 7 per side (*Acris crepitans*). In funnel-mouthed larvae, these papillae are consolidated into a massive ridge on each side. A smaller ridge is developed in *Ptychohyla leonhardschultzei* and to a still lesser extent in *Centrolenella fleischmanni* and *Agalychnis callidryas*.

The median ridge defines the back of the postnarial arena. The ridge has a curved, pointed, or straight margin in most tadpoles examined and in ones illustrated by other authors; although the pattern is rather species-specific, from looking across the samples it is clear that there is a continuous spectrum of possible shapes for this structure. In *Hyla mixe*, *Centrolenella fleischmanni*, *Anotheca spinosa*, and *Ptychohyla schmidtorum* the median ridge is reduced to a tall papilla. In *Megophrys minor*, the ridge is replaced by a large, nipple-shaped, projection; a similar but much smaller projection occurs in *Colostethus nubicola*.

Serrations or fine papillae often occur on the free ventral margin of the median ridge in tadpoles with a wide ridge. When the median ridge is relatively large it is often covered with pustulations or a secondary serrated ridge on its anterior surface.

Because of the medial position of the postnarial arena, this collection of projections, together with the tongue anlage, may be important in dividing up the respiratory current into right and left streams. This is not to say that the papillae are without additional possible functions such as the sensory role implied by Kenny.

LATERAL RIDGE PAPILLAE

The structures which I have called the lateral ridge papillae are developmentally associated with the postnarial and buccal roof arenas. When these arenas are reduced or absent, the lateral

ridge papillae invariably are reduced or absent. Increases in the number and size of arena papillae vary directly with increases in the size of the lateral ridge papillae. However, the papillae are absent in all Orton Types 1, 2, and 3 larvae that I examined.

The papillae may be simple and cylindrical with minor terminal and anterior pustulations or secondary papillae (e.g., *Hyla regilla*, *H. dendroscarta*, *Acris crepitans*, and *Anotheca spinosa*); or they may be rather huge flaps with long, finger-like, marginal papillae (e.g., *Hyla mixe*, *Ptychohyla leonhardschultzei*, *Oreolalax*). There are all grades between these extremes. In funnel-mouthed larvae the lateral ridge papillae are thick, stout projections lacking secondary papillation.

Kenny (1969b) illustrated the lateral ridge papillae of *Hyla geographica* as being rather small flaps with jagged margins. Savage's (1952) illustration of these structures shows them to be of the rather huge "hand-like" variety in *Bufo bufo*. In general, large lateral ridge papillae seem to be associated with the stream habitat.

These papillae could have any or all of the functions suggested for oral papillae elsewhere in the mouth—sensory, respiratory, or mechanical (as interceptors of feeding currents). Their position in front of the buccal pockets and their relatively large size in tadpoles that ingest coarse material (e.g., stream forms; see Ecological Considerations) offer some support to a mechanical interceptor hypothesis. This does not rule out other functions.

BUCCAL ROOF ARENA

The buccal roof arena has already received attention under the heading of Buccal Floor Arena and only a few comments are added here.

Anterior BRA papillae are positioned medially to the anterior BFA papillae; thus, buccal roof arenas tend to be more elongate and rectangular than buccal

floor arenas. The number of BRA papillae correlates directly with the number of BFA papilla although there are never as many roof as floor papillae (maximum number observed was 34 in *Ptychohyla leonhardschultzei*). When the BFA is reduced, the BRA generally diminishes. In *Colostethus nubicola* the BRA papillae are reduced in height and coalesced into ridges.

BRA papillae are, typically, simple cones. They are rarely bifurcated or decorated with terminal pustulations.

Although all the authors mentioned above as providing illustrations of post-narial structures included some or all of the buccal roof proper in their drawings, their illustrations appear incomplete in regard to post-median ridge features. As to size, shape, number, and position of the accuracy of the representations of buccal roof arena papillae cannot be determined, because independent descriptions of these structures are not provided.

The possible functions for the BRA papillae are treated above with those of the BFA papillae.

GLANDULAR ZONE AND DORSAL SECRETORY PITS

Few generalizations can be made about the size and shape of the glandular zone. Some tadpoles which clearly are not specialized for microphagy (e.g., *Microhyla heymonsi*, *Anotheca*) completely lack a visible glandular zone in the stages that I examined. In other tadpoles the zone is interrupted medially (e.g., *Rhinophrynus*, *Microhyla ornata*, *Leptobrachium oshanensis*) or extremely reduced in that region (e.g., *Megophrys minor*, *Oreolalax*, *Leptobrachium hasselti*, *Hyla rufitela*). The glandular zone was, on the average, proportionately wider in *Hyla mixe*, *Hyla saraya-cuensis*, and the megophrynine pelobatids than in *Hyla regilla*. It was narrower in *Ptychohyla*, *Smilisca*, and *Gastrotheca*. The anterior margin of the zone was so indistinct in *Hyla phlebodes*,

H. ebraccata, and *Centrolenella* that its length could not be determined. The posterior extension of secretory pits onto the dorsal velum and pressure pads is highly variable.

Kenny (1969b) illustrates the glandular zone of *Hyla geographica* as divided medially. In *Xenopus laevis* and *Pipa* (Sokol, 1977a), the glandular zone is largely restricted to the individual pressure pads (Wassersug, unpublished scanning electron micrographs) but may extend far anterior to the pressure pads in *Xenopus tropicalis* (Sokol, pers. comm).

Whereas the shape and size of the total glandular zone fails to reveal patterns that can be easily associated with function, phylogeny, or ecology, the secretory pits themselves do reveal such patterns. *Ascaphus truei* has irregularly shaped, poorly defined pits that are much smaller than those of *Hyla regilla*. *Bombina* is similar to *Ascaphus*, but has well defined pits, at least along the anterior margin of the glandular zone. Other tadpoles with smaller pits than those of *Hyla regilla* include *Centrolenella fleischmanni*, *Hyla phlebodes*, *H. mixe*, *H. ebraccata*, and *Ptychohyla leonhardschultzei*. None of these species is believed to be particularly microphagous. On the other hand, a list of tadpoles with secretory pits much larger than those of *Hyla regilla* include *Hyla rufitela*, *Agalychnis callidryas*, *Gastrotheca riobambae*, *Rhinophrynus dorsalis*, *Microhyla berdmorei*, *Scaphiopus bombifrons*, and *Xenopus laevis*. These are all tadpoles that, based on the totality of characters examined and their known behavior and ecology, should be as efficient as, if not more efficient than, *Hyla regilla* in microphagous suspension-feeding. Thus there seems to be a weak inverse relationship between the size of the secretory pits and the typical size of the particles upon which a larva feeds. There also seems to be a loose inverse correlation between the size of secretory pits and their density; the density of the

secretory pits is reduced in forms with good microphagous abilities such as *Rhinophrynus*, *Microhyla berdmorei*, *M. ornata*, and *Scaphiopus bombifrons*, compared to more typical pond larvae.

Feeding currents are directed against the glandular zone by the ventral velum, particularly when the velum is in a partially elevated position. Kenny (1969a) called this region the "dorsal food traps" and considered the glandular zone a primary site for mucous entrapment of food particles. In the earlier discussion of secretory pits on the ventral velar projections, I hypothesized a possible mechanism for the generation of mucous strands from the glandular zone. Kenny has suggested that the ventral velum may actually push particles onto the zone during valvular closure. There can be little question that food is in one way or another trapped in mucus along the zone, for in some specimens flocculent matter can be found adhering directly to this surface.

Whether the glandular zone is a primary region for food entrapment is another question. In specimens where particles were adhering to the glandular zone, they were also adhering to the branchial food traps and were in far greater abundance on the latter surfaces. Massive accumulations of particulate matter on the glandular zone would prevent normal valvular closure. For the valve to be operational when there is substantial mucous entrapment on the glandular zone, mucus and food aggregates must be swept off the surface with efficiency and regularity.

Hypothetically, there are other possible functions for the mucous secretion of the glandular zone besides food entrapment. Mucus may be important for proper valvular function of the ventral velum. Both lubricant (Gradwell, 1970) and sealant (Kratochwill, 1933) roles have been proposed for this secretion in relation to the valvular operation of the ventral velum.

DORSAL VELUM

Of the species I examined, the only one which completely lacks a dorsal velum is *Anothea spinosa*. In a few others, the dorsal velum appears vestigial (e.g., *Hyla phlebodes* with its two, tiny, lateral flaps). In pipids, which lack a valvular ventral velum, the dorsal velum is also absent.

In most species the dorsal velum is distinct and is divided into right and left halves. The few species in which the velum is continuous across the midline include *Ascaphus truei*, the microhylids, *Centrolenella*, *Hyla rufitela*, *H. femoralis* and tadpoles of the *Hyla leucophyllata* species group. In species where the velum is broadly interrupted medially, the free medial edges are often reflected posteriorly, leading into the esophagus.

In Orton Type 3 tadpoles, the velum is shorter than in *Hyla regilla*. The velum is also distinctly shorter than that of *H. regilla* in *Rhinophrynus*, *Centrolenella*, *Agalychnis*, *Hyla ebraccata*, *Hyla sarayacuensis*, *Ptychohyla schmidtorum*, *Smilisca sordida*, and the megophryine pelobatids (with the possible exception of *Leptobrachium hasselti*). The only species in which the velum is unquestionably longer than that of *H. regilla* are *Microhyla berdmorei*, *Microhyla ornata*, and *Scaphiopus bombifrons*.

Papillae occur along the free medial margin of the dorsal velum in *Ptychohyla* and the megophryine pelobatids. Although they were not seen in *Hyla mixe*, these papillae may be common in suctorial, stream larvae of Orton Type 4. *Alytes* shows some papillation in this region of the velum. These papillae have not been discussed or illustrated previously; presumably, they serve a sensory or mechanical straining function, but these are mere speculations.

At present it is not possible to associate the size of the dorsal velum with other aspects of the biology of any group of tadpoles.

There are two schools of thought

concerning the primary function of the dorsal velum. These schools are identifiable with the two names given this structure, viz., "dorsal velum" and "posterior filter valve." Among the latter school, Kratochwill (1933) holds that the dorsal velum, in conjunction with the pressure cushions, functions as the posterior half of the valve system that seals off the filter chambers from the buccal cavities. Kenny (1969a) has essentially the same view, although he does not believe that closure is complete. Since microhylids have a ventral velum partially anchored to tops of the filter plates (fully anchored at the top of cb. 4), Gradwell (1974) has argued that a valvular function is essential for the dorsal velum in these larvae. Savage (1961), as a proponent of the "velum" school, proposes that the major function of this fold is to deflect currents down into the filter cavities in such a way that vortices form in the branchial baskets between the individual filter plates. DeJongh (1968), who also used the term "velum" sees this structure as having a protective function. In his view that when the ventral velum is in its down position, the dorsal velum is pulled taut and prevents water from flowing directly along the ciliary groove where it could displace mucous strands. Although it is obvious (and was recognized by Kratochwill) that the dorsal velum could act both as a valve and a velum, topographically at least, a velar function is obligatory for this structure. In accepting a velar function, I am not accepting all the details of Savage's centrifugal feeding mechanism. Indeed, the objections that Kenny (1969a) raised to Savage's centrifugal feeding theory seem completely valid.

PRESSURE CUSHIONS

Pressure cushions were regularly damaged in dissection and will not be discussed in detail. Overall, the cushions show a very strong correlation in size and shape with the size and shape of the branchial baskets. For example,

when the branchial baskets are elongate, the pressure cushions are elongate (e.g., microhylids, *Agalychnis*, *Rhinophrynus*); when the filter plates of the second and third ceratobranchials are reduced so that there is a single filter cavity on each side, there is also a single pressure cushion on each side (pelobatids).

When the filter cavities are extremely large, as in *Rhinophrynus*, *Xenopus* (Sterba, 1950), and *Pipa* (Sokol, 1977a), there are three rather than two distinct cushions on each side. Sokol (1977a) reports another oddity in *Pipa parva*; this is the occurrence of papillae at the anteroventral corners of the huge pressure cushions of this genus.

The function of the pressure cushions is not clear. Kratochwill (1933) assumed that they could abut tightly to the filter surfaces and actually push water through the filters on the expiration half of each pumping cycle. This seems doubtful, considering the delicate nature of these pads, although I concede that in living tadpoles fluid pressure may make these structures stiffer than they appear in preserved larvae. A stronger objection is that a single cushion rarely fills a whole filter cavity.

The pressure cushions have also been thought to serve as a protective rim for the ciliary groove. Although the posterior margin of the cushions makes up the anterior margin of the ciliary groove, far more tissue is involved in the cushions than is necessary to demarcate the groove. Thus, I doubt that this is the sole function of the cushions.

Although I cannot offer a completely satisfying hypothesis for the function of the cushions, I suspect from the common occurrence of scattered secretory pits on these surfaces that they are involved in direct contact with food matter. A possible role in lifting food from the filters was mentioned above.

SYSTEMATIC CONSIDERATIONS

"Tadpole morphology represents perhaps one of the most useful and most

misused of the available character complexes to be used in frog classification." (Lynch, 1971:200).

An effort is made here to discern shared, derived characters among internal oral features that either substantiate or refute traditional taxonomic schemes. No formal effort is made to reassign any taxa, since such activities cannot be justified solely on the basis of larval characters. Species are discussed by family in the same order in which they are presented in the Descriptions.

Results from this study generally support traditional systematic assignments at the familial and lower taxonomic level. Suprafamilial relationships are discussed separately in the section titled Phylogenetic Considerations.

ASCAPHIDAE

Ascaphus larvae have many features which distinguish them from all other tadpoles, including the direct-developing *Leiopelma* embryos. Although I have not personally examined *Leiopelma* ontogenetic series from the genus have been described by Stephenson (1950a, 1950b, 1955). In comparing Stephenson's figures and description with my figures and description of *Ascaphus* I can find no common, clearly derived features in these genera. In the absence of shared, derived characters it may be concluded that early developmental stages do not provide any evidence for grouping *Ascaphus* and *Leiopelma* in the same family. I support Savage (1973) and Goin *et al.* (1978) in recognizing two families, the Ascaphidae and the Leiopelmatidae (*contra* Duellman, 1975).

DISCOGLOSSIDAE

Lanza, Cei and Crespo (1975, 1976) have argued on the basis of immunological data for partitioning the Discoglossidae into the Bombinatoridae (with *Bombina*) and the Discoglossidae (with *Discoglossus* and *Alytes*). Except in some fine points of lingual papillae pattern,

the three genera have very similar larval oral structures.

Certain of their shared features, such as expanded internal narial flaps and the pharyngeal shape, warrant including these genera in the same family on strictly phenetic grounds. I consider it unlikely that these similarities are due to convergence. The features in question may be primitive ones for anurans and of little use in discerning sister groups. If much weight, however, is given immunological data, we may find grounds for splitting the Archaeobatrachia as currently recognized into several additional families.

RHINOPHRYNIDAE

Although *Rhinophrynus dorsalis* larvae share certain features of other families, such as an exposed glottis on the floor of the mouth (à la Microhylidae) and the full attachment of the ventral velum to the dorsal margins of the second and third filter plates (à la Discoglossidae), they are overall unlike any other tadpoles examined and completely justify the monotypic assignment of this species.

MICROHYLIDAE

At the familial level it is clear that the microhylids are tightly united and, at the same time, separate from all other frog families by the uniqueness of their larvae (Orton, 1957). Although Savage (1952, 1955), Nelson and Cuellar (1968), and Gradwell (1974) have all described larval oral features in a variety of microhylid genera, their descriptions are neither detailed enough nor comparative enough to help determine whether internal oral features can be useful in discerning relationships within this family. Of the three species of *Microhyla* I examined, *M. ornata* and *M. berdmorei* are extremely similar. Considering the large number of superficially similar species in the genus (Parker, 1934) it is doubtful that the minor oral features used to distinguish these two species would separate either of them

from all other species in the genus. The funnel-mouthed form, *M. heymonsi*, however, is immediately separable from the rest of the genus (with the possible exception of the other known funnel-mouthed species, *M. achatina*) in both external and internal features. It is doubtful that any other free-swimming microhylid larvae are much like *M. heymonsi* in oral features; *M. achatina* and *M. heymonsi* may be justifiably removed from the genus *Microhyla*, if any weight is given to their larval characters.

PELOBATIDAE

The shallow filter plates of cb. 2 and cb. 3 and the bowl shape of the branchial baskets are unique features shared by all pelobatid larvae examined and the family is easily justified on these features. Three major subfamilial groups can be seen in the material at hand, and the European pelobatids may form a fourth division. *Megophrys* stands apart from the other pelobatids because of adaptations associated with the funnel-mouth. It forms the first division. The second division consists of the nonfunnel-mouthed megophrynines represented here by *Leptobrachium* and *Oreolalax*. Tadpoles of these genera are sufficiently similar in larval morphology to justify their separation from *Megophrys* (Inger, 1966). The third division consists of *Scaphiopus*, which is grossly different from the other pelobatids. Many of these differences may relate to the fact that these are temporary pond dwellers rather than inhabitants of streams.

HYLIDAE

Although the hylid larvae examined were few compared to the number of species in this family, the sample was originally selected because of its ecological diversity, and consequently demonstrated much correlated morphological diversity (see Functional Considerations and Ecological Considerations). Given this great morphological diversity, few unique features emerge which might

define the family. Whether there are any larval features unique to the Hylidae cannot be determined until more tadpoles of other advanced families are studied. At present it seems that all hylids have a basically similar pattern of attachment for the ventral velum. Moreover, all have perforated, slit-like or oval internal nares. But comparison with descriptions in the literature for other families, such as the Ranidae and Bufonidae, and my own preliminary observation of leptodactylid larvae, suggest that these are not unique features; alone they will not distinguish the hylids from most other neobatrachian families.

Recently there has been much work on the subfamilial systematics of the Hylidae. Duellman (1970) associated the genera *Anotheca* and *Gastrotheca* in the subfamily Amphignathodontinae, while Maxson (1977) has argued from immunological data that *Anotheca* more appropriately belongs in the hyline subfamily. Both *Anotheca spinosa* and *Gastrotheca riobambae* share a generally robust habitus and have the medial portion of the ventral velum deflected by a large laryngeal disc. The large laryngeal disc in both species probably results from independent convergence on early lung use. The larva of *Anotheca spinosa* is otherwise so bizarre that oral structures are of little use in establishing its subfamilial status.

Maxson (1976) has also used immunological data to argue for elevation of the Phyllomedusinae to familial status. The one phyllomedusine larva that I examined, *Agalychnis callidryas*, differs from all the other hylids in many features (e.g., the shape of the prepocket buccal surface, buccal floor arena, velar margin, and filter apparatus), but is virtually identical to *Phyllomedusa trinitatis* as illustrated by Kenny (1969a). Considering the extreme similarity among phyllomedusine tadpoles in gross external morphology (for Central American species, see Duellman, 1970), behavior, and ecology (Starrett, 1973;

Wassersug, 1973), we may safely conclude that internal oral features of *A. callidryas* are typical for the subfamily. Phyllomedusine tadpoles as a group seem to be more specialized for suspension feeding (*contra* Kenny, 1969a) than other hyliid larvae. Whether this warrants their separation from the Hylidae at the family level cannot be determined at this time.

At least three species of *Phyllomedusa*, *P. guttata*, *P. cochranæ* and *P. jandaia* are funnel-mouthed forms (Bokermann and Sazima, 1978) with a particular external morphology regularly associated with a complex internal morphology unlike that seen in *P. trinitatis* or *A. callidryas*. If further examination of funnel-mouthed phyllomedusines reveals the typical internal specializations of other funnel-mouthed larvae, this may warrant placing them in their own genus. If, however, they show the specializations for microphagy characteristic of other phyllomedusine larvae, then, collectively, the uniformity and uniqueness of the phyllomedusine larvae may support the elevation of the subfamily to family status.

Distinguishing features of the larvae of the four genera of Hyline frogs, *Ptychohyla*, *Hyla*, *Smilisca*, and *Acris*, are all of a quantitative rather than qualitative nature. There is as much difference between species within the genera *Ptychohyla* and *Hyla* as there is between members of all four genera. *Hyla regilla*, *Acris crepitans*, and *Smilisca sordida* are all very similar and show the generalized "pond" tadpole pattern for internal oral structures.

Ptychohyla schmidtorum and *P. leonhardschultzei* differ from one another at least as much internally as externally, completely supporting the separation of these forms into the two species groups, *P. schmidtorum* and *P. euthysanota*, respectively (Duellman, 1970).

All species groups within *Hyla* recognized by Duellman (1970) appear valid according to the features I have examined. A case can be made, how-

ever, for elevating the rank of some of these groups (see below).

H. rufigata is the northernmost member of the *Hyla albomarginata* species group, and has a larva externally like typical pond *Hyla* such as *H. regilla* (*H. eximia* species group) except for its 2/4 denticle pattern. But internally, certain features such as the narial vacuities and the transverse row of papillae on the buccal floor, justify supraspecific separation of this *Hyla* from the other *Hyla* in this study. Unfortunately, not enough is known about other members of the *albomarginata* species group to say whether these features are diagnostic of the group in general. *Hyla dendroscarta* (*H. bromeliacia* group) has a variety of oral features which again would separate it from more typical pond *Hyla* larvae. Likewise, the similarity between *Hyla ebraccata* and *Hyla sarayacuensis* justifies their separation from the other forms. *H. ebraccata* and *H. sarayacuensis* form a closely united group readily distinguishable in their oral anatomy from all other tadpoles examined; similarities in their larval morphologies completely justify their association in the *Hyla leucophyllata* species group. Equally divergent from the basic pond hyline type are *H. mixe* (*H. mixomaculata* group) and *H. phlebodes* (*Hyla microcephala* species group). In the shape of its branchial baskets and gill filter density, *Hyla femoralis* likewise stands apart from the other *Hyla* examined, including the Holarctic *H. regilla*. Maxson and Wilson (1975, Table 4) reach the same opinion based on albumin similarities.

If one general conclusion can be reached from the diversity of larval oral structures in *Hyla*, it is that the genus is an artificial group that warrants fragmentation into several genera. There is no question that, if adult frogs showed as much diversity in oral structures as these tadpoles do, herpetologists would have partitioned them into separate genera decades ago.

On the other hand, there are no unique features of *Smilisca* or *Acris* tad-

poles that would help to define these genera as distinct from *Hyla*. Maxson and Wilson (1975) considered *Acris* as very different from *Hyla* at the organismal level (based on karyotypic and adult osteological characters; cf. Duellman, 1970 and Gaudin, 1974) but wrote, "A protein-based classification would include [*Acris*] in the same taxonomic category as the North American *Hyla* species but exclude many South American species currently placed in the genus *Hyla*." In this conflict of organismal versus molecular evolution the tadpoles appear to support the systematic arrangement derived from protein structure rather than the one based on adult characters. According to Maxson and Wilson's data for two Holarctic *Hyla* that I examined, *Hyla regilla* is more similar to *Acris* than it is to *Hyla femoralis*. Again, this similarity is borne out by tadpole oral characters. In terms of both molecular structure and larval anatomy, *Acris* is more similar to certain species of *Hyla* than are many species of *Hyla* to each other. The oral morphology of hyline tadpoles provides the first anatomical support for systematic patterns formulated from molecular data. For this reason tadpole structures deserve consideration in future work on anuran taxonomy.

DENDROBATIDAE AND CENTROLENIDAE

Of the two families remaining, there are no internal oral features that readily distinguish the dendrobatid larvae from other advanced families. The differences between *Colostethus subpunctatus* and *Colostethus nubicola* are massive and, again, if internal oral features of the larvae are taken into consideration, the funnel-mouthed form could justifiably be separated into a different genus.

Features that are unique to *Centrolenella fleischmanni* are virtually all associated with the extreme elongation of the tadpole (e.g., elongated internal nares, elongation of the second and third ceratobranchials). Considering

that elongation is a general characteristic of centrolenid larvae, these internal features probably characterize the family and serve to distinguish these larvae from tadpoles of other families.

EVOLUTIONARY CONSIDERATIONS

THE *Ascaphus* AND *Leiopelma* LIFE CYCLES

Despite their extreme specialization for life in torrential streams, *Ascaphus* larvae have all the essential, anatomical features for suspension-feeding (Wassersug, 1975). They have, for example, well developed gill filters. Although the filter mesh in *Ascaphus* is not nearly as dense as in typical pond forms, the filters are more fully developed than in certain other stream forms that clearly had pond-inhabiting ancestors (e.g., *Ptychohyla*). *Ascaphus* larvae have expanded ceratohyals that can serve as a buccal pump and a ventral velum that can act as a valve to maintain one-way flow to the branchial food traps. Although they lack secretory ridges in the pharynx they have otherwise well-developed branchial food traps (Wassersug and Rosenberg, 1979). These larvae have functional narial valves. The filters, buccal pump and valves are all essential features of the tadpole suspension-feeding mechanism (Wassersug, 1975).

Experimental work has shown that *Ascaphus* tadpoles can extract food particles from suspension (Altig and Brodie, 1972), although their efficiency (in terms of the particle sizes they capture) is below that of more typical pond forms (Wassersug, 1972). As noted by Gradwell (1973) and Starrett (1973), there is no support for the popularly accepted (cf. Morton, 1967:42) suggestion by Noble (1927) that these larvae take in most of their food through their nares.

Some authors (Eaton, 1959; Schmalhausen, 1968) have considered the stream tadpoles of *Ascaphus* to repre-

sent the generalized anuran larva. This view is based on an effort to explain the hard mouth parts of tadpoles as a generalized feature initially evolved as an aid for hanging onto rocks in streams. Such a view is founded on the belief that the most generalized extant frog must have the most primitive tadpole. Hard mouth parts in most other tadpoles are primarily used to generate a suspension of food particles, and it is equally plausible that they did not initially evolve as a response to life in streams. As with other organisms, an anuran may be a mosaic of primitive and derived characters; there is no real reason why a frog and its larva must be at the same grade of specialization. It seems most likely that *Ascaphus* tadpoles are secondarily specialized for stream life.

Developmental series of *Leiopelma* have not been available for study. Stephenson (1950a, 1950b), who has examined ontogenetic material of this genus, believed that the direct-developing embryo of *Leiopelma* represented a link between the salamander and frog type larva. Stephenson (1955) wrote that, "no evidence exists of terrestrial specializations as shown by certain anurans which have secondarily acquired a terrestrial mode of development following abandonment of a specialized aquatic tadpole's stage." In direct contrast to that statement, it is generally accepted by most workers that *Leiopelma* secondarily acquired direct development from a free-swimming tadpole stage.

From my analysis of Stephenson's (1950a) reconstruction of the embryonic chondrocranium and visceral arches of *Leiopelma* larvae, it is fair to say that this genus shows a substantial number of vestigial features, ones specifically associated with an aquatic, suspension-feeding existence. The jaw suspension in developing *Leiopelma* is directed anteroventrally and only secondarily rotates at metamorphosis into a more

vertical position. The midportion of the ceratohyal is expanded in the frontal plane as it is in all aquatic larvae with a buccal pump. Long ceratohyals associated with the filter plates of suspension-feeding forms line the otherwise nonfunctional gill slits. In fact, what Stephenson identified as a branchial pouch in his serial sections (1950a, Plate 1), may be a vestige of the ciliary groove used to transport particles trapped in mucus to the esophagus in suspension-feeding tadpoles. In contrast, *Eleuthero-dactylus*, a direct-developing frog that no one doubts evolved from an aquatic ancestor, shows far fewer features associated with feeding in its jaw suspension and branchial skeleton than *Leiopelma* (See Lynn, 1942). Evidently, *Leiopelma* arrived at terrestrial development from an ancestor with an aquatic, suspension-feeding, larva.

EVOLUTIONARY TRENDS IN THE DISCOGLOSSIDAE

A case can be made for grouping *Ascaphus* closely with the discoglossids. These forms are similar not only in the way the ventral velum attaches to the filter plates, but also in the gross shape of the buccal floor arenas, the position of the glottis, and the absence of a well-developed ridge pattern for the secretory tissue of the branchial food traps (Wassersug and Rosenberg, 1979).

The multiple pustulations on the tongue anlage in *Alytes* are similar to the multiple papillation of the tongue anlage in *Ascaphus*. In features of the pharynx, it is *Bombina* among the discoglossids which is most similar to *Ascaphus*. Typical advanced tadpoles have well organized ridges running transversely across the branchial food traps, and pits along the posterior margin. *Ascaphus* and *Bombina* lack both the secretory pits and ridges that characterize the branchial food traps of most "advanced" anuran families (e.g., hylid, bufonid, ranid). *Alytes* and *Discoglossus*, in contrast, have secretory cells clus-

tered to form ill-defined pits. The microanatomy of the food traps suggests a morphological sequence going from *Ascaphus* to *Bombina* to *Alytes* and *Discoglossus* and then to more advanced anuran larvae. Phylogenetically, the secretory pits evidently appeared before secretory ridges (Wassersug and Rosenberg, 1979).

These ideas neither support nor conflict with the proposal of Lanza, Cei and Crespo (1975, 1976) to partition the Discoglossidae (*sensu lato*) into two families. Sokol (1977b) recognizes the suborder Discoglossoidei, to encompass the two families Leiopelmatidae (= *Ascaphus* and *Leiopelma*) and Discoglossidae; the similarity of *Ascaphus* tadpoles to discoglossid larvae makes this an eminently reasonable association.

THE PIPOIDEA AND THEIR RELATIONSHIPS

Since Orton (1957) first proposed that *Rhinophrynus* and the Pipidae were closely related, virtually all herpetologists (except for Griffiths and de Carvalho, 1965) have formally or informally recognized the superfamily Pipoidea. It is thus surprising how little resemblance exists between oral structures in *Rhinophrynus* tadpoles and pipid larvae. The shape of the prepocket buccal surface, the presence of a valvular ventral velum, the shape of the branchial food traps, the shape of the dorsal velum and pressure cushions, all distinguish *Rhinophrynus* larvae from any pipid genus. This does not necessarily mean that *Rhinophrynus* is not closely related to the pipids at the superfamilial level or that Orton's Type 1 larva is invalid. Starrett (1968, 1973) and Sokol (1975, 1977a) have both reaffirmed the validity of the *Rhinophrynus*-pipid association. *Hymenochirus*, *Xenopus* and *Pipa* larvae all differ so much from each other that, provided they are validly grouped at the familial level, *Rhinophrynus* could still be reasonably united with them at the next higher level.

Certain features of *Rhinophrynus* are

similar to the discoglossids; most conspicuous is the full attachment of the ventral velum to filter plates cb. 2 and 3. *Rhinophrynus*, however, has advanced upon the discoglossid grade in having developed secretory ridges in the branchial food traps (Wassersug and Rosenberg, 1979). In several superficial features, *Rhinophrynus* closely resembles the microhylids. These include: buccal floor exposure for the glottis; absence of posterior projections from the velar margin; branchial food traps restricted to the anterior portion of the filter cavities (crescentic organs); larger branchial baskets with a denser filter mesh; and the absence of postnarial and buccal roof papillae. Except for the buccal floor exposure of the glottis, the restricted size of the branchial food traps and the density of the filter mesh, this combination of character states is not unique to *Rhinophrynus* and the microhylids; it occurs, for instance, in certain hylids. Although the glottis is exposed in *Rhinophrynus* and microhylids, its position is much farther forward in the microhylids than in *Rhinophrynus*. In other features, such as the overall shape of the visceral skeleton, the resemblance breaks down. Presumably, similarities between *Rhinophrynus* and microhylids are due to convergence on a largely suspension-feeding, nectonic way of life.

If we accept *Rhinophrynus* as a pipoid, then it follows that *Rhinophrynus* has, overall, the most generalized Orton Type 1 larva. This view is based on the belief that the absence of a valvular velum in the Pipidae is best comprehended as a derived character. There is little support for the opposite hypothesis offered by Gradwell (1975a), which would derive virtually all anurans from the genus *Xenopus*. The unusual position and microanatomy of the secretory ridges in *Xenopus* (Wassersug and Rosenberg, 1979), the papillate pressure cushions and fused filter rows in *Pipa*, and the complete loss of filter-feeding structures in *Hymenochirus*, must all be

highly derived characters. Sokol (1977a, 1977b) has reached a basically similar conclusion with an independent analysis of these and other characters.

Within the Pipidae, the genera *Xenopus* and *Pipa* bear the strongest resemblance in larval oral surface structures (Sokol, 1977a). On the basis of other characters, however, Sokol places *Hymenochirus* closer to *Xenopus*. According to Sokol the filter apparatuses of *Xenopus* and *Pipa* are extremely different, although one must concede that they are more similar to each other than either is to *Hymenochirus*. Sokol views *Pipa* as evolving away from the extreme microphagous condition, as exemplified by *Xenopus*. *Pipa* appears to be a dietary specialist adapted for feeding on medium-sized planktonic organisms. *Hymenochirus*, of course, is a carnivore, specialized for feeding on large planktonic organisms.

Except for discoglossoid frogs, all anurans including the Pipodea have a fused trigeminal and facial ganglia. Sokol views this as a uniquely derived character and Lynch (as pers. comm. in Sokol, 1977b) has gone so far as to suggest that the Pipodea are derived from pelobatoid frogs.

It is my suspicion that the fusion of the fifth and seventh ganglia is an indirect result of the orientation of the palatoquadrate bar in non-discoglossoid larvae and is associated with perfection of a suspension-feeding larva with a large, efficient buccal pump. Investigators as far back as Luther (1914; see Edgeworth, 1930; Wassersug, 1975) have explained the unusual chondrocranium of tadpoles as an adaptation associated with their feeding mechanism. Elongation and anterior extension of the palatoquadrate has allowed for expansion of the ceratohyal in the horizontal plane to form the piston of the buccal pump (Severtzov, 1969). The anterior displacement of the palatoquadrate, however, limits the area for the emergence of cranial nerves from the brain

case in the region between the optic cup and the otic capsule. We may hypothesize that evolution has "squeezed" the ganglia of the fifth and seventh nerves together incidental to the forward displacement of the palatoquadrate and expansion of the ceratohyal. The palatoquadrate of the pipids is unlike that of the other anuran larvae, but it nevertheless has a relatively anterior position compared to discoglossoid larvae. Considering the differences in the form of the palatoquadrate in pipoid frogs and non-pipoid, non-discoglossoid larvae, it seems possible that an efficient ceratohyal pump has evolved along two paths above the discoglossoid grade. One path would have been through the Pipodea and the other through all remaining anurans. It seems plausible that the trigeminal and facial nerves could have been independently "squeezed" together on both evolutionary courses.

In conclusion, the Pipodea are an extremely specialized and diverse superfamilial group. Internal oral features corroborate Sokol's conclusion that the Pipodea are too specialized to be either an ancestral anuran group, or near the ancestral line (*contra* Starrett, 1973). However, in identifying the pipoid larvae as highly specialized and derived, I consider it premature to propose that they evolved from any extant family or superfamilial group.

THE MICROHYLID PROBLEM

Perhaps the greatest controversy in the higher taxonomy of the Anura centers on the position of the frogs with the Orton Type 2 larvae, the Microhylidae. Many authors have commented on this problem, most recently Starrett (1973), Savage (1973), Sokol (1975), Duellman (1975), Lynch (1973), and Blommers-Schlösser (1975). Based on the characters used by Orton and Starrett, the microhylids bear the closest resemblance to the pipids and *Rhinophrynus*. Based on characters of the adults and additional larval features discussed by Sokol,

the microhylids are presumed to be ranoid-derived frogs.

In the structure of their branchial food traps and visceral skeleton, microhylid larvae are neither clearly pipoid nor obviously ranoid. The buccal floor exposure of the glottis in the microhylids is most like that of the pipids, but the attachment of the ventral velum is more similar to that of advanced Type 4 larvae. My study suggests that the microhylid larvae are profoundly different from both Orton Type 1 and Orton Type 4 larvae.

Of the microhylids examined (see also Savage, 1952), *Microhyla heymonsi* looks the most like an Orton Type 4 larva in internal oral features. Specifically, it has a relatively long buccal floor anterior to the buccal pockets, small branchial baskets (compared to other microhylids), and a ventral velum virtually continuous across the midline. There is little question that these resemblances are due to secondary convergence as the ancestor of *M. heymonsi* abandoned total reliance on microscopic food. The presence, however, of a continuous or at least nearly continuous ventral velum in this species raises the possibility that microhylids could have evolved from forms with a continuous ventral velum. This excludes the *Pipidae* (but not *Rhinophrynus*).

The ancestor of the Microhylidae need not be from an extant family. If microhylid larvae evolved from tadpoles with keratinized beaks, the presence of secretory ridges in the branchial food traps points to an origin above the discoglossoid/pelobatoid grade. Blommers-Schlösser (1975) recently described larvae of *Pseudohemius granulatus*, a scaphiophrynine frog from Malagasy; these tadpoles exhibit a mosaic of microhylid/ranid features in their external anatomy. As more exotic microhylid larvae are described, I suspect that they will support a microhylid-ranoid relationship, and resemblances between microhylid larvae and pipoid forms will prove to be convergences.

THE ORIGINS OF THE "ADVANCED" ANURANS (TYPE 4 LARVAE)

Although it is generally recognized that pelobatoid frogs (families Pelobatidae and Pelodytidae) represent the least specialized families with Orton Type 4 larva (Lynch, 1973), the relationship of these frogs to more advanced families is not fully understood. Duellman (1975) placed the pelobatoid frogs in his suborder Archaeobatrachia, suggesting that they are closer to the "ancestral" frogs than to the "advanced" anurans of the order Neobatrachia. Pelobatids lack secretory ridges in the branchial food traps and in that feature are most similar to the archeobatrachian *Ascaphus* and discoglossids (Wassersug and Rosenberg, 1979).

The most detailed discussion to date on the origin of Type 4 larvae is in Heyer (1975:40-43). Savage, as a *pers. comm.* in that paper, suggests that leptodactylids arose directly from a leiopelmatid ancestor. Heyer (who evidently accepts the Starrett-Savage tenet that the pipoid larvae represent the ancestral larval form) correctly points out that one implication of Savage's suggestion is that the Type 4 larva must have evolved twice from a beakless ancestor. Extant archeobatrachian species with their relict distributions and exotic larvae provide little information that can help evaluate Savage's suggestion. To quote Heyer (1975:42), "The crux of the argument hinges, then, on whether the pelobatid acosmanuran tadpole is really the same as a leptodactyloid (bufonid and ranoid) acosmanuran tadpole." Heyer argues that given a limited number of ways that a tadpole can be efficient at scraping, one would not expect great differences in morphology between pelobatid tadpoles and leptodactyloid larvae, even if they are diphyletic.

I am not so convinced that the Pipoidae are the stem anuran group (see above), and, if they are not, this alters the problem. Nevertheless, assuming that the pelobatids and leptodactyloids

arose from families with beaked larvae, the question of the phylogenetic relationship of the leptodactyloids to archeobatrachian frogs remains.

Lynch (1973) has made a case for the evolution of primitive leptodactylids directly from megophryine pelobatids.¹ I have not examined internal features of any leptodactylid tadpoles in detail but these tadpoles seem superficially similar to other neobatrachian, Type 4 larvae. The bow-shaped branchial baskets and abbreviated attachment of the ventral velum to the filter plates of the second and third ceratobranchials appear to be uniquely derived characteristics of the pelobatids and may preclude deriving the pattern of velum attachment in other Type 4 larvae from this family. I feel that it is most plausible that the pelobatid velar structure evolved from the common Type 4 pattern. If Australian myobatrachine larvae have pharyngeal morphology like the megophryine pelobatids I would consider this strong evidence for the phylogeny proposed by Lynch. Until more is known about primitive leptodactylid (*sensu lato*) larvae, it is best to view the pelobatids as a sister group rather than the ancestors of more advanced frogs.

EVOLUTION OF SPECIFIC LARVAL TYPES IN THE GENUS *Hyla*

Because of the large and morphologically diverse sample of *Hyla* larvae examined it is both possible and appropriate to comment on the adaptive radiation of larval types in this genus. The evolution of two types are singled out for discussion, the macrophagous herbivorous larva and the arboreal larva. These types help demonstrate how knowledge of larval morphology can give some insight into evolutionary history below the familial level.

1) *Macrophagous, Herbivorous Hyla larvae*.—Members of the *Hyla leucophyl-*

lata species group, *Hyla ebraccata* and *Hyla sarayacuensis*, exhibit larval specializations away from ultra-planktonic suspension feeding and toward macrophagy. They have reduced or lost the papillae of the buccal floor and roof. They have a low filter mesh density and abbreviated branchial food traps. *H. sarayacuensis* has a lower number of filter rows and more reduction of the secretory ridges in the branchial food traps than *H. ebraccata* and appears to be the more macrophagous of the two forms.

Of all the hyline tadpoles studied, *Hyla phlebodes* (*Hyla microcephala* species group) larvae have the most extreme reduction in structures associated with the ingestion of fine, suspended matter.

If one looks at the general pattern of reduction, a morphological sequence can be drawn from *Hyla regilla* as a typical *Hyla* larva to the *leucophyllata* group and then to the *Hyla microcephala* group as represented by *Hyla phlebodes*. This morphological sequence represents a trend toward a particular type of macrophagy dealing with coarse plant matter and detritus rather than large, live prey such as eaten by carnivorous tadpoles. It is through a similar morphological series that the ancestors of the *Hyla microcephala* group might have evolved, although I do not mean to imply that the *Hyla microcephala* group evolved directly from the *Hyla leucophyllata* group.

2) *Arboreal Hyla Tadpoles*.—The internal anatomy of *Hyla dendroscarta* larvae sheds some light on the question of how arboreal forms of the *Hyla bromeliacia* group may have evolved. Duellman (1970:681) stated that the "group containing *bromeliacia* in northern Central America and *dendroscarta* in southeastern Mexico, apparently diverged from the lowland pond-breeding *picta*-stock by adapting to arboreal breeding habits in a successful attempt

¹ Lynch (as cited in Sokol, 1977a) suggested that the pipoids could also be derived from the pelobatoids, but I consider this unlikely for the reasons stated above.

to invade the foothills in low mountains where ponds are scarce." Members of the *H. picta* group, however, are quite different in larval biology from *H. dendroscarta* and *H. bromeliacia*. *H. picta* larvae have a tall tail fin, moderately short pointed tail, and occur in grassy pools. Tadpoles of the *H. bromeliacia* group have the long tails of stream adapted larvae. Internally, *H. dendroscarta* larvae have a mosaic of features that are associated with either pond or stream existence. The lobe-like infralabial papillae and absence of velar marginal projections are characteristic of certain pond tadpoles. On the other hand, the many tall buccal floor and buccal roof papillae and the truncation of the third filter cavity are features that appear in stream larvae. In overall internal and external proportions, *H. dendroscarta* tadpoles are more like stream than pond larvae.

Duellman (1970:429) noted that members of the *H. bromeliacia* group have cranial characters similar to *H. miotympanum* but considers any alliance between these two species tenuous. In fact, members of the *H. miotympanum* group have stream larvae that look very much like tadpoles of the *H. bromeliacia* group. *Hyla arborescendens*, the sister species of *H. miotympanum*, even has larvae with the unusual 2/4 denticle pattern that characterizes the middle American arboreal *Hyla* larvae. A species of *Hyla* closely related to the *H. miotympanum* group has a breeding behavior that could represent a link between the stream breeding of *H. miotympanum* and the arboreal breeding of *H. dendroscarta* and *H. bromeliacia*. This is *Hyla thorectes*, which, according to Duellman (1970, p. 391), has stream larvae but "is unique among members of the genus in northern middle America by depositing its eggs on vegetation above the streams." It seems most plausible that the ancestor of the present bromeliad breeding *Hyla* went through just such an evolutionary stage, first leaving eggs

above water, that dropped into the water after hatching, then later developing tadpoles that could survive on the vegetation. This is a more believable evolutionary sequence than the quantum jump from pond to tree that is required if the *Hyla bromeliacia* group evolved from a *Hyla picta*-like stock.

Arboreal larvae in other genera and families, particularly those with elongate larvae, could have followed a similar evolutionary history. Centrolenid larvae presumably represent an intermediate stage in this evolutionary scenario.

The present geographic range of *H. miotympanum*, *H. arborescendens*, and *H. thorectes* does not exclude the possibility that their immediate, common ancestor could also have served as the ancestor of the *H. bromeliacia* group. Based on external and internal morphology of the larvae and the breeding behavior of the adult, it is highly probable that the ancestor of *H. bromeliacia* species group separated from the nuclear central American hyloid stock at the level of a common branch leading to *H. miotympanum*, *H. arborescendens*, and *H. thorectes*.

THE EVOLUTION OF ONTOGENIES AND ITS ROLE IN LARVAL DIVERSITY

While this study demonstrated a great deal of morphological diversity in the feeding structures of anuran larvae, it is worth noting that few truly unique structures were seen in any of the tadpoles.

Most differences between species are gradational differences in the relative size, shape, or number of particularly common features.

Three specific processes can account for most of the structural diversity: proliferation, fusion, and reduction. These are not only processes in the phylogeny of anuran larvae, but are common processes in their ontogeny as well. Recently, much attention has been given the role of ontogenetic shifts in phylogenetic evolution (Gould, 1977); the tadpole

oral structures helped to illustrate how important this heterochrony may be in generating evolutionary diversity.

The opportunity for heterochrony in anuran evolution is accentuated by the fact that developmental programs can be modified not once, as in most vertebrates' development, but twice. They can be modified first when the embryo develops into a tadpole, then again when the tadpole metamorphoses into the frog.

In comparing different forms, it is sometimes possible to tell which part of the developmental process has been distorted through evolution. Consider, for example, the different patterns for the gill filters seen in hylid larvae with reduced branchial baskets. Both *Hyla phlebodes* and *Anotheca spinosa* have small branchial baskets with highly reduced gill filters. In the case of *Anotheca* the filters are thin, wispy structures, whereas in *H. phlebodes* they are blunt, knoblike projections. In the normal ontogeny of a *Hyla regilla* both morphologies are seen (Wassersug, 1976b and *pers. obser.*). In the early ontogeny, as the embryo develops into a larva, *Hyla regilla* gill filters appear relatively knobby without having a complicated, folded pattern. At metamorphosis, however, as the filters degenerate, they shrink and develop a wispy appearance, much like those of *Anotheca*. We can suggest that the reduction of the gill filters in *Hyla phlebodes* results from abnormally early and prolonged metamorphosis of the gill filters relative to other oral structures. It then follows that the pattern seen in *Anotheca* is due to an arrested embryonic development of these same organs.

Other examples can be seen in the papillae of the buccal floor and roof. The proliferation, attenuation and bifurcation of buccal papillae commonly seen in stream bottom larvae with suctional mouths suggests differential growth of these structures either by early, accelerated growth or by prolongation of the period over which they develop. The fusion of papillae into

ridges, a common pattern in funnel-mouthed forms, suggests a relative suppression of the tendency for the papillae to elongate, without a reduction in the tendency for papillae bases to grow and develop.

Some of the most unusual morphological patterns described in this paper can be comprehended in the framework of heterochrony. A choice example is the uninterrupted gill filter rows that bridge the gill slits in *Gastrotheca*. Although it is possible that this pattern is due to a truly novel fusion of filter rows, there is an ontogenetically simpler hypothesis. I suspect that when the gill pouches develop in the embryo they perforate only at the bottom of the filter canal and these perforations fail to coalesce into continuous slits. Arrested development of the larval gill slits in free-living *Gastrotheca* may be precursory to direct development in *Gastrotheca* larvae that have abandoned the free-living tadpole stage. This hypothesis, one of arrested development, could be verified or refuted with a growth series of *Gastrotheca* embryos.

Major advances in our general understanding of anuran larval diversity will require attention to subtle differences in ontogenetic processes.

ECOLOGICAL CONSIDERATIONS

TADPOLE FEEDING ECOLOGY

The autecology of anuran larvae is poorly known. Much of what is discussed here constitutes hypotheses presented in relatively broad terms. For instance, the sizes of food particles are referred to simply as "small," "medium," or "large." This vague, comparative rather than quantitative, terminology is necessitated by our ignorance. There is little hard information on the actual particle size distribution either in the environments in which tadpoles occur or in their alimentary tracts.

The typical pond larvae is often described as a filter feeder (Griffith, 1961; cf. Savage, 1973); but elsewhere I (Was-

sersug, 1975) have argued that the broader term "suspension-feeder" is more appropriate. As demonstrated by Rubenstein and Koehl (1977) filter feeding, that is, sieving, is only one mechanism by which aquatic organisms can extract particles suspended in water. Aerosol engineers have identified at least five mechanisms by which particles can be removed from a fluid. Depending on the physical properties of the suspended particles and the entrapping structures (e.g., particle diameter; mass; pore size of filters; electrostatic charge, etc.), certain mechanisms will be more effective than others.

Tadpoles can clearly ingest particles smaller than the pore size of their gill filters (see Dodd, 1950; Jenssen, 1967; Kenny, 1969a; Hendrick, 1973; Wassersug, 1972), so they must use other mechanisms besides simple sieving. Kenny (1969b), Wassersug (1972), Wassersug and Rosenberg (1979), have all discussed mucous entrapment in tadpoles. This process may involve inertial impaction or electrochemical attraction (electrostatic entrapment; cf. Rubenstein and Koehl, 1977; LaBarbera, 1978). Following Rubenstein and Koehl, it is likely that tadpoles capture particles by at least three methods: direct interception, inertial impaction, and electrostatic entrapment.

Although many herpetologists have made a distinction between the feeding ecologies of tadpoles with and without keratinized mouth parts, there may be little or no difference between the way in which these animals feed. It is fair to say that *all* free-living tadpoles, except for some extremely specialized macrophagous forms, can suspension-feed. Tadpoles with hard mouth parts may also graze on periphyton, macrophytes, and large detrital material, but their grazing activity primarily serves to produce a suspension. This suspension is then handled internally by basically the same mechanisms that tadpoles lacking hard mouth parts use.

PARTICLE SORTING: THE GENERAL MECHANISM

The complexity of internal oral structures in anuran larvae suggests that complex sorting processes take place between the oral orifice and the esophagus. The variety of palps, flaps, papillae and other projections in the tadpole mouth are interpreted here as forming a multi-tiered sorting system used to capture particles of a variety of sizes with great efficiency.

The sorting starts at the oral orifice. Particles too large to enter the mouth cannot be ingested unless they are reduced to smaller particles by the beaks and denticles. Particles small enough to enter the mouth may be too large to pass between the infralabial papillae and can be ejected immediately.

Particles small enough to pass the infralabial papillae enter the space between the buccal floor and buccal roof arena. From this region there are three possible courses a particle can take. If the particle is too large to pass between any of the papillae of the buccal floor, it can be coughed out of the mouth. Presumably, all particles rejected would be too large to pass down the esophagus. If a particle is too large to go between the papillae on the right and left side of the arena, but small enough to pass between the papillae at the back of the arena, the general funnel-like shape of the buccal floor arena will shunt it directly posterior and into the esophagus. Any particle small enough to pass between the papillae laterally can go to either the left or right side and over the ventral velum into the pharynx.

Once in the pharynx, a particle may be trapped by direct interception and inertial impaction on the gill filters. Particles so small as to pass through the gill filters can still be aggregated in mucus on the branchial food traps. The larger aggregates formed there can then be retained by the gill filters (Wassersug, 1972).

How particles trapped in the filter

cavities are transported posterolaterally to the ciliary groove and ultimately to the esophagus is poorly understood. A reasonable, but admittedly vague, hypothesis is that particulate matter compressed between the pressure cushions and the gill filters is shunted laterally by a rhythmic pulsing action of the pharynx. It should be possible to test this hypothesis by giving tadpoles dyed food and sacrificing them individually at successively longer intervals after feeding. Dissection of these larvae should reveal the path of food through the pharynx and clarify the transport mechanism. In any case it is evident that tadpoles have alternative methods of trapping particles that depend on particle size. The ingestive system appears arranged so that gross structures which can trap large particles protect smaller, more delicate surfaces which are designed for handling the finer particles. Specifically, buccal structures protect the branchial baskets from clogging by channeling larger particles, that have already passed through the infralabial papillae, directly to the esophagus.

It follows from the above general outline that interspecific differences in the size, shape, and spacing of the various trapping structures will reflect differences in the particle sizes upon which different larvae feed most efficiently.

MICROHABITAT IMPLICATIONS OF MORPHOLOGICAL PATTERNS

Several common morphological patterns in the overall proportions of the various sorting and sieving structures of tadpoles provide clues to the feeding ecologies of these organisms. Many of these patterns were alluded to in the section on Functional Considerations and are summarized here.

Several anurans have larvae which show a loss or reduction in all of the particle sorting and trapping structures. This morphological pattern is consistently associated with extreme macrophagy, as illustrated by the carnivorous *Ano-*

theca and *Hymenochirus* larvae. Not only obligate carnivores, but several herbivore/detritivore larvae have abandoned indiscriminate suspension-feeding in favor of macrophagy. *Hyla microcephala* and *Ooeidozyga* larvae are examples.

Another common pattern is the proliferation of buccal sieving structures in larvae which also have reduced filter density (high filter porosity). This places emphasis on the gross sieving structures rather than finer entrapping surfaces and appears to be an adaptation for feeding on a relatively coarse suspension of particles. Benthic, thigmotactic tadpoles commonly show this pattern.

Fusion of buccal floor and roof papillae into ridges, which is characteristic of funnel-mouthed tadpoles, enables the buccal cavity to serve as a particle guiding system, rather than a particle sieving system. This morphological arrangement appears ideal for handling a relatively narrow size range of moderately coarse particles.

Enlargement of the branchial baskets and a very high density of the gill filters is most often associated with relatively few, widely spaced buccal papillae. Tadpoles with this pattern appear well adapted for feeding on a suspension of uniformly small particles. Indeed, larvae with this morphology are the obligate microphagous suspension-feeders; *Microhyla ornata* and *Xenopus laevis* are two examples.

Each of these patterns correlates well with the distribution of particle size in the environments where the larvae exhibiting them live. For example, microplanktonic algae are likely to be rare in the aphotic environment of *Anotheca spinosa*. Food source in this habitat will be those large organisms near the top of the food chain, on which *Anotheca* is clearly specialized to feed.

Benthic, thigmotactic tadpoles are best represented by stream larvae. Stream environments are relatively oli-

gotrophic; with a rapid exchange of water, and constant nutrient washout, there is little chance for a phytoplanktonic bloom in a stream. Most primary productivity in this habitat is in the form of periphyton, which can be gleaned only by grazing upon the substrate. The grazing activity of tadpoles with beaks and denticles produces a relatively coarse suspension of particles.

Tadpoles adapted for feeding on these self-generated suspensions are not likely to encounter large particles or exceptionally small particles with any frequency. Although it may appear advantageous for stream tadpoles to have large and dense gill filters that could completely retain all of the smallest particles ever encountered, extremely small food particles are too rare in a stream habitat to warrant the energetic cost of developing and maintaining the tissues necessary for capturing all such particles. At the other extreme, thigmotactic stream larvae are not likely to run into very large particles such as those regularly ingested by macrophagous carnivores and herbivores. The large gap at the back of the buccal floor and buccal roof arena, which allows many tadpoles to shunt the largest particles they ingest directly from the buccal cavity into the esophagus, is absent in these forms.

The funnel-mouth adaptation appears even more specialized for selecting relatively large particles in a relatively narrow size range. Lacking the multi-tiered sieving system, funnel-mouthed tadpoles have abandoned the ability to feed indiscriminately over a broad range of particle sizes in favor of the capacity to handle large particles which might float in the backwashes of quiet streams or adhere loosely to surfaces.

Tadpoles specialized for extreme microphagy seem to occur most commonly in midwater in small, stagnant pools or ponds which have high insolation, a high nutrient load, and an abundance of unicellular phytoplankton (see Heyer, 1973, 1974; Wassersug, 1973). These

microphagous suspension-feeders often metamorphose at a relatively small size and quite soon after hatching. They are specialized for ingesting the earliest, primary productivity which develops in temporary ponds, namely small phytoplankton. The absence of keratinized mouth parts in most of these forms can be construed as an energy-conserving adaptation. While hard mouth parts would allow these larvae to graze on macrophytes, periphyton, and other detritus, such material is often absent in their ephemeral environment and these morphological structures are energetically expensive to develop and maintain.

A few tadpoles are unusual in appearing to be specialized for handling food of two different size classes. *Scaphiopus* and *Rhinophrynus* typify this bimodal size selection potential. They are both temporary pond breeders in seasonally dry areas. In these environments much of the potential food is either unicellular algae or the larger herbivores, such as conspecifics, that graze on this algae. On the one hand, these larvae are efficient, ultraplanktonic suspension-feeders able to handle the initial phytoplanktonic blooms in the small bodies of water where they breed. On the other hand, the ephemeral nature of their ponds requires that they be able to grow to a large size extremely fast and this means they must be able to ingest all other possible food items in their ponds. In having few, widely spaced, buccal floor papillae and dense gill filters, these larvae are adapted for handling both the largest and the smallest particles in their environment; they are not likely, however, to feed efficiently on the medium sized particles that most tadpoles generate while grazing.

In contrast to the extreme forms just described, the majority of pond larvae appear adapted for handling a relatively broad spectrum of food sizes and types. In the "average" temporary pond (e.g., a temporate zone, vernal pond) the size

distribution of potential food can fluctuate so drastically that most larvae would never reach metamorphosis if they ate food in a narrow size range only. Because of extreme fluctuation in the resource base it is not surprising that there has been little documentation of direct (exploitation) competition among tadpoles for food. Competition among most anurans has resulted in spatial and temporal separation of larvae rather than overt dietary partitioning (Heyer, 1974, 1976). Only recently has exploitation competition been demonstrated for typical pond larvae in either the laboratory (Steinwascher, 1978; Seale and Beckvar, in press) or the field (Seale, 1973).

One can use slight variations in the morphological patterns delineated above to hypothesize about the feeding ecologies of specific anuran larvae. *Hyla rufitela* and *Hyla femoralis*, for instance, which have denser gill filters than either *Hyla regilla* or *Acris crepitans*, are probably more efficient at ultraplanktonic entrapment than these latter forms. As another example, the *Bufo* larva illustrated by Savage (1952) has many tall buccal floor papillae, a feature associated with benthic, thigmotactic grazing. It is not surprising, then, that *Bufo* tadpoles are often found feeding on the bottom, grazing on detritus. They appear specialized for handling medium to small fragments of material and may not be particularly efficient at feeding on either extremely large or extremely small particles.

From all that has been said so far, we can conclude that tadpole oral features reflect the breadth of the larval diet, at least in terms of particle size, and, as indicators of niche breadth, oral structures can provide some insight into species packing problems for tadpoles. To illustrate this latter point we can compare two distinct larval ecotypes. Larvae of moderately large size from cool-temperate climates (e.g., many ranids) require a relatively long developmental time, over which they are likely

to be exposed to a very broad range of particle sizes. They may have few potential competitors for food resources and are understandably dietary generalists. In contrast, in wet, lowland, tropical ponds developmental time can be rapid but the anuran fauna is very large, and competition for breeding sites severe (Crump, 1974, and others cited therein). This is a situation where many anuran species use the same breeding pond at the same time and the larvae may not be able to avoid competition; here one is most likely to find pond tadpoles which are dietary specialists.

Consider *Hyla phlebodes*; the extremely specialized oral morphology in this larvae and its obligatory, narrow dietary range suggest that it occurs in ponds with larvae of many other species that use other parts of the resource base. Contrast this with *Gastrotheca riobambae*—based on its generalized morphology this large larvae would appear to have a very broad diet and to feed efficiently on a variety of food types. One can predict that it would occur with larvae of relatively few other species. Although I have personally collected neither species, Duellman (pers. comm.) has indeed confirmed that *H. phlebodes* larvae are always found inhabiting ponds with tadpoles of several other species, while *G. riobambae* (which occurs at high elevation) is found alone.

The feeding currents of a tadpole are also its respiratory currents, so it is appropriate to add here some comments on ecological patterns in the respiratory systems of anuran larvae. Tadpoles that are specialized for feeding on large particles often have a large, exposed glottis on the floor of the mouth and evidently depend extensively on aerial respiration. It is a reasonable hypothesis that, in the absence of buccal papillae to act as coarse sieves, these larvae should reduce their aquatic respiratory pumping activity in order to prevent accidental clogging of the filter cavities or glottis by particles that would otherwise be too

small to be ingested. Macrophagous larvae, such as *Anotheca*, probably do not exhibit regular aquatic pumping. It is known that *Hymenochirus* larvae do not exhibit regular respiratory pumping and only open their mouths to take in either air or prey (Sokol, 1962). Many of the macrophagous, herbivorous *Hyla* larvae (*H. microcephala* and *H. leucophyllata* species group) are small and may rely extensively on cutaneous respiration.

Obligate midwater, microphagous anuran larvae often occur in extremely eutrophic and, potentially hypoxic, habitats; they also exhibit large glotta and may depend heavily on aerial respiration.

In contrast, stream larvae, which live in well aerated habitats, can depend on gill and cutaneous respiration to meet their metabolic needs. In these forms, aerial respiration could lead to positive buoyancy, which may be maladaptive (Wilder et al., 1920; Wake, 1966; Wassersug and Seibert, 1975).

Differences in both feeding and respiration are often reflected in the relative size of the buccal floor since buccal floor area is one parameter affecting the volume displaced by the buccal pump (Wassersug and Hoff, 1979). This, in turn is intimately related to both feeding and respiratory patterns.

All macrophagous larvae exhibit a general expansion of the buccal floor in the prepocket region relative to the rest of the floor and pharynx that allows them to suck in large particles. This

expansion is well exemplified by the differences between the funnel-mouthed *Microhyla* and other *Microhyla*. Most *Microhyla* have a small buccal displacement compared to the large volume of their branchial baskets. These non-funnel-mouthed forms cannot completely clear the oral cavity with a single stroke of the buccal pump, but can maintain a continuous, gentle flow past the gills throughout a buccal cycle. Thus, they are equipped to clear constantly a suspension of rather fine matter, as well as to irrigate continuously their respiratory surfaces. In contrast, *M. heymonsi*, with its comparatively large buccal pump and small branchial baskets, can suck in a large volume of water with each stroke of the buccal pump. *H. heymonsi* has the ability to use gape-and-suck feeding to selectively take in rather large particles but not to maintain a gentle continuous respiratory flow while it is feeding. Its relatively large buccal pump displacement is well adapted for sporadic feeding, but could cause the animal to lurch conspicuously forward and backward in the water column if the tadpole pumped maximally during normal respiratory activities.

More work on the feeding and respiratory ecology of anuran larvae will be necessary before we will completely understand the ecological and evolutionary implications of larval morphology. It is, however, already clear that knowledge of tadpole oral morphology can provide major insight into the way of life of these organisms.

SUMMARY AND CONCLUSIONS

This study has been limited to gross surface features in the mouths of tadpoles—surfaces where particles are extracted from water currents and gas exchange takes place. Internal oral surfaces are described for larvae of eight anuran families. When combined with descriptions elsewhere in the literature, the anatomy of this region is now known for representatives of a dozen families.

In the following pages the morphological variation seen in the oral structures of the larvae examined is first summarized, and morphological patterns reviewed. Then major conclusions concerning anuran systematics and tadpole evolution and ecology are enumerated.

MORPHOLOGICAL VARIATION

An effort was made to interpret the

function of all major morphological structures:

(1) *Keratinized spurs and projections*.—Two keratinized structures are seen inside the mouths of certain tadpoles. The first, which occurs in many species and may be used in shredding food is a bilateral, medially directed keratinized spur at the edge of the oral orifice between the upper and lower beaks. The second, a medial cornified projection from the prenarial arena in the macrophagous *Scaphiopus bombifrons*, is presumably used in holding and shearing prey.

(2) *Infralabial papillae*.—In thigmotactic, benthic larvae these are typically large, elongated and dendritic, whereas, in larvae adapted for macrophagy, they may be short and globose or lacking altogether. These structures have a mechanical and possible chemoreceptive function; they appear particularly important in the positioning of food as it comes into the mouth.

(3) *Lingual papillae*.—Most species examined have two premetamorphic papillae, but some have one or four. *Ascaphus* and the discoglossids have multiple lingual papillae. The pipids, lacking a tongue, also lack lingual papillae. Following Hammerman (1969), I have assumed these structures serve a chemoreceptive function.

(4) *Buccal floor arena (BFA) and Buccal roof arena (BRA) papillae*.—Papillae of the buccal roof and floor are usually arranged to form a V- or U-shaped area. Species may have no buccal papillae (e.g., Pipidae, macrophagous Hylidae) or as many as eighty or more papillae on the buccal floor alone. Papillae seem to be important in the primary sorting and sieving of particles from the water; they may actually be the major food sorting structures in the mouth of stream-adapted species.

In funnel-mouthed larvae, papillae often are either absent or fused into interlocking dorsal and ventral ridges. I interpret these structures as chutes for separating out larger food particles.

(5) *Ventral velum*.—The ventral velum is an important valve which regulates one-way flow from the buccal to the pharyngeal cavity in all anuran larvae except the Pipidae. There are six major configurations of the ventral velum which can be associated with specific families or superfamilial groups.

(6) *Gill filters*.—Interspecific variation, in overall size and in relative density of the gill filters reflects differences in tadpole feeding ecology. Tadpoles generally recognized as extremely specialized for microphagy have very large branchial baskets and large filter plates with very dense gill filters; these serve to extract oxygen and food from the water. Obligate macrophagous larvae have reduced branchial baskets and gill filters; in the extreme macrophagous forms, such as *Hymenochirus*, gill filters are completely absent. Funnel-mouthed larvae typically show some reduction in the gill filters compared to close relatives with more typical oral features.

Two unusual patterns involving fusion of filter rows are documented. In *Pipa*, neighboring filter rows on each filter plate are fused so that the filter canal between the rows is canopied. In *Gastrotheca*, the filter rows are fused ventrally with opposing filter plates over the ventral gill slits, which means that they have fenestrated gill pouches rather than continuous gill slits.

(7) *Branchial food traps*.—There are two basic patterns for these organs; one characterizes the Archaeobatrachia (*sensu* Duellman, 1975), and the other the Neobatrachia. Overall size and shape of the branchial food traps does not seem to correlate strongly with any aspect of tadpoles' diets. The texture of the secretory surface itself, however, shows some correlation with larval feeding ecology. Forms specialized for microphagy tend to have distinct, widely spaced ridges, while extreme macrophagous larvae tend to lose the secretory tissues in general, and the secretory ridges specifically. Exceptions to the 2 basic forms are the unique secretory

ridge patterns seen in *Rhinophrynus*, *Xenopus*, and the Microhylidae. *Ascaphus* and the discoglossids have an extensive field of secretory epithelia in the branchial food traps but lack secretory ridges (see Wassersug and Rosenberg, 1979, for details of the micro-anatomy of these surfaces).

(8) *Glottis*.—The size of the glottis and the extent of its exposure on the floor of the mouth appears to correlate both with aerial respiration and the tadpole's buoyancy. Bottom larvae tend to have a small glottis, while obligate mid-water larvae, and those that depend heavily on aerial respiration (e.g. *Anotheca*), invariably have a large glottis.

(9) *Esophageal funnel*.—The size and shape of the anterior portion of the esophagus reflect the size of the particles upon which tadpoles commonly feed; macrophagous larvae tend to have a large esophagus, whereas obligate microphagous forms have a small, narrow esophagus.

(10) *Prenarial arena*.—Diverse species-specific patterns in ridges, pustulations, projections, etc. are found in the prenarial arena of anuran larvae. Their exact function is not well understood but it is hypothesized that they assist the lower beak in holding and positioning food as it enters the mouth.

The most distinctive pattern for these structures is seen in funnel-mouthed forms, regardless of family; here there is invariably a distinct, posteriorly directed, V-shaped ridge in the prenarial arena.

(11) *Internal nares*.—The internal nares are perforated structures in all but microhylid larvae. Their orientation seems to vary, in part, with the shape of the tadpole head. The nares are always associated with valves. In the Discoglossidae, large flaps extend under the nares and presumably protect them from particles flowing into the mouth. Several species have pockets of presumed sensory epithelia (Jacobson's organs) arising from the margins of the internal nares. Sensory epithelium is evi-

dent in the unperforated nares of the Microhylidae. Tadpoles of this family have a stiff flap that extends down from the posterior margin of the internal nares and may help direct currents toward these sensory regions.

(12) *Postnarial arena*.—Tadpoles typically have a symmetrical arrangement of papillae or ridges that are tightly grouped posterior to the internal nares. Projections are large and numerous in this region in forms which have many large and numerous buccal papillae elsewhere in the mouth. Postnarial structures, however, are reduced in forms which typically lack papillae or show reduction in papillae elsewhere on the buccal roof or floor. Blunt, shallow papillae typically replace rows of postnarial papillae in the postnarial arena of funnel-mouthed larvae.

Postnarial papillae are aligned to form a cap over the lingual anlage when the mouth is closed. Postnarial structures may serve chemoreceptive, mechanical-receptive, and particle-sorting roles. They may be important in directing water currents to regions of sensory epithelia and particulate matter to other regions of the buccal cavity for sorting.

(13) *Glandular zone*.—The ventral velum of tadpoles meets the buccal roof during closure along a region of secretory epithelia, the glandular zone, which has been implicated in particle capture. The secretory tissue of the zone may assist the branchial food traps in aggregating particulate matter in mucus. There appears to be a slight inverse correlation between the size of the secretory pits in the glandular zone and the particle size that a tadpole typically feeds upon. It is proposed here that the glandular zone may also assist the velum in its valvular function. The zone varies extensively in shape, but in part reflects the shape of the ventral velum beneath it. Secretory tissue of the glandular zone often continues posteriorly onto the pressure cushions of the dorsal pharynx. Macrophagous larvae often lack a glandular zone.

(14) *Dorsal velum*.—A continuation of the ventral velum onto the roof of the mouth is characteristic of all non-pipid tadpoles but is reduced in extreme macrophagous forms. The dorsal velum is invariably positioned slightly posterior to the ventral velum in such a way that it must deflect water from the buccal cavity into the anterior part of each filter cavity when the buccal floor is elevated. It is proposed here that, in deflecting water currents ventrally and anteriorly, the dorsal velum helps prevent the resuspension of particulate matter aggregated and precipitated in the posterior parts of the pharynx.

(15) *Dorsal pharynx*.—The dorsal region of the pharynx is small in all tadpoles, and the only gross structures of this region are pressure cushions. These are folds of epithelium that extend ventrally and complement the shape of the filter cavities below. The larger and deeper the filter cavities are, the larger and deeper are the pressure cushions. The secretory tissue on these structures suggests that they have a role in food processing. They may help collect food in the filter cavities or in some way assist in the lateral movement of food from the filter epithelium to the ciliary groove.

SYSTEMATIC CONCLUSIONS

Major points from the discussion on Systematic Considerations are summarized below in the framework of the Archaeobatrachia-Neobatrachia distinction. Patterns in oral structures generally support but in some cases refute, prevailing ideas on the taxonomic relationships within and among anuran families.

(1) Internal oral features of *Ascaphus* larvae and *Leiopelma* embryos provide no evidence for the inclusion of these genera in the same family.

(2) When considering the structure of their internal nares and the shapes of their pharynxes, the current members of the Discoglossidae appear to form a

natural family or superfamily. Branchial food trap anatomy suggests a close relationship between *Ascaphus* and the Discoglossidae. Among the Discoglossidae, *Bombina* appears to have the most generalized larva.

(3) *Rhinophrynus* larvae are externally similar to *Xenopus* and *Pipa*, but internally they are as different from pipid larvae as they are from the larvae of any other family. While the superfamilial association of the Rhinophrynidae and the Pipidae may be valid, *Rhinophrynus* must be accepted as the most generalized of the Pipoidea.

Pipoid frogs are so specialized that the superfamily could not serve as the immediate ancestors of any extant anuran families. The recent suggestion that the Pipoidea is more closely related to the Neobatrachia than to the Archaeobatrachia (cf. Sokol, 1976b) finds no support in my observations.

(4) Many features of the ventral velum, branchial food traps, internal nares, and glottal position distinguish the Microhylidae from all other families. Internally, microhylid larvae do not look like pipid tadpoles, although their branchial food traps are grossly similar to those of *Rhinophrynus*. Ranoid rather than pipoid associations of the Microhylidae are suggested by larval features (specifically, the shape of the ventral velum in *Microhyla heymonsi*).

(5) The Pelobatidae have larvae which are unique in the shape of their branchial baskets and the attachment of their ventral vela. The absence of secretory ridges in this family is consistent with an Archaeobatrachian assignment (cf. Duellman, 1975). I interpret the shape of the branchial baskets in the Pelobatidae as a unique, derived character state, which makes it unlikely that other anuran families evolved directly from this family. Primitive leptodactylid (e.g. myobatrachian) larvae, however, have not been examined and if their branchial baskets are of the pelobatid form, this will support the idea

that leptodactyloid frogs have their origin in Asiatic (megophrynine) pelobatids.

(6) Interspecific variation in oral structures in the Hylidae is enormous. Most patterns can be interpreted along ecological lines. Externally similar larvae from different genera are often very similar internally, suggesting convergencies or parallelism. On the other hand, tadpoles of the same genus which differ only slightly in external morphology, may differ greatly in internal morphology. The following are systematic conclusions at the subfamilial level:

(a) *Anotheca* and *Gastrotheca* are extremely different in internal larval morphology, supporting Maxson's (1977) removal of *Anotheca* from the Amphignathodontinae. However, *Anotheca* larvae are so bizarre, they provide little evidence for inclusion of this genus in the Hyliinae.

(b) Tadpole oral structures support the idea that *Phyllomedusa* and *Agalychnis* are closely related but do not settle the issue of the status of the family Phyllomedusidae.

(c) *Hylinine* larvae with similar ecologies are internally very similar, regardless of genus or species.

(d) Internal oral features support certain phylogenetic relationships previously suggested by biochemical data only, and which otherwise conflict with traditional taxonomy based on adult osteology. An example is the similarity between *Acris crepitans* and *Hyla regilla* larvae compared to certain other *Hyla* tadpoles. The basis for this "tadpole: biochemical" taxonomic congruence is not well understood, and more tadpoles will have to be studied to know whether it is a general pattern.

(e) The genus *Hyla* is artificial and should be partitioned into several genera. Certain taxa such as the *Hyla mixomaculata* and *Hyla microcephala* species groups, probably form valid genera.

EVOLUTIONARY CONCLUSIONS

In addition to the specific taxonomic

considerations just reviewed, some general evolutionary conclusions may also be drawn from this work.

(1) The unusual chondrocranium of tadpoles is associated with the development of an expanded ceratohyal and an efficient buccal pump. The development of an enlarged buccal pump, the presence of an elongated ceratohyal, and the presence of a buccal valve in anuran larvae are all features interpreted as associated with a generalized suspension-feeding way of life. This is considered the primitive and generalized way of life for anuran larvae.

(2) A unique way of life for anuran larvae, not specifically discussed by herpetologists in the past, is macrophagous herbivory. Extreme reduction in the branchial food traps, loss of buccal papillation, development of large, pad-like infralabial papillae, and the presence of a massive buccal floor area characterize these tadpoles. This morphology, best exemplified in *Hyla phlebodes*, is interpreted as an adaptation for feeding on coarse plant matter and detritus. Larvae of the *Hyla leucophyllata* species group show moderate development of this type of larva. *Ooeidozyga* in the Ranidae has independently converged on this morphology.

(3) The arboreal larvae of the *Hyla bromeliacia* group evolved from an ancestor with a stream-adapted larva. It is suggested that the elongated arboreal larvae, in general, had stream-adapted ancestors, and that the *Hyla bromeliacia* group specifically evolved from a lineage that was ancestral to *Hyla miotympanum*, *H. arborescandens*, and *H. thorectes*.

(4) Much of the anatomical difference between larvae of different species can be explained by heterochronic changes in the early (embryonic) and late (metamorphic) ontogeny of the tadpoles. Certain morphological patterns can be identified as due to evolutionary modifications of specific early or late ontogenetic events when compared with more generalized larval developmental patterns. Further understanding

of the evolution of anuran larvae diversity will require greater knowledge of differences in larval ontogenies than is presently available.

ECOLOGICAL CONCLUSIONS

The majority of internal oral features in tadpoles are interpreted as part of a multi-tiered particle entrapping system which sorts ingested particles by size. Direct interception and inertial impaction are used to different extents on different surfaces. The mucous surfaces of the branchial food traps and the gill filters of the pharynx together can efficiently trap the smallest particles ingested by a typical pond larva. Buccal papillae strain larger particles from the water and funnel them directly to the esophagus, bypassing most of the pharynx. Delicate pharyngeal surfaces that could be clogged or damaged by large particles are, thus, protected by this size-sorting mechanism.

The size of the particle upon which a species feeds most efficiently may be inferred from the size, shape, number and spacing of buccal and pharyngeal structures. Interspecific differences in these features may reflect differences in the size distribution of particles in the microhabitats in which the tadpoles live.

In comparison with generalized tadpoles, extreme macrophagous larvae show reduction in all pharyngeal structures associated with planktonic entrapment. On the other hand, extreme microphagous larvae, which live in mid-water, have large branchial baskets and dense gill filters well designed for capturing small phytoplankton that many abound in their habitat. Benthic, thigmotactic larvae typically inhabit streams which are probably devoid of phytoplankton but rich in periphyton. These

larvae can generate a coarse suspension with their keratinized mouth parts; they have closely spaced, supernumerary buccal papillae for straining coarse particles, but highly porous gill filters not well adapted for ultraplanktonic entrapment. Funnel-mouthed tadpoles feed selectively on large particles floating on the water surface; they have buccal ridges in place of papillae that seem well adapted for sorting moderately coarse particles from a relatively narrow size range.

Most pond larvae are adapted for handling the broad spectrum of food types and sizes that may occur in unpredictable environments. Pond larvae specialized for ingesting a narrow size range of particles (e.g., *Hyla phlebodes*) are most likely to occur in species rich environments where competition may have been intense during their evolution.

Respiratory structures vary with the availability of dissolved oxygen. Since the amount of phytoplankton in any aquatic body affects the amount of dissolved oxygen, there appears to be a relationship between a tadpole's diet and its respiratory structures. Oligotrophic streams are likely to be well-aerated, and the benthic tadpoles from these environments tend to have few of the morphological features associated with aerial respiration. On the other hand, obligate midwater microphagous larvae may live in extremely eutrophic ponds, and typically have a large glottis, a feature associated with a strong dependence on aerial respiration.

Internal oral structures of anuran larvae can be used to make reasonably sound predictions about the feeding and respiratory ecology of anuran larvae when field data are not available.

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APPENDIX: GLOSSARY OF TERMS

Most terms used in this monograph are explained briefly here; fuller descriptions and definitions are provided for the majority of terms in Wassersug (1976a). Morphological variation for internal oral features listed here is reviewed under "Functional Considerations" in the Discussion section of this paper.

Advanced tadpoles—Orton's Type 4 larvae.

Anterior filter valve—see ventral velum.

Anterior narial papillae—papillae arising from the anteromedial corner of the internal nares and projecting posteroventrally over the narial passage.

Arboreal tadpoles—any larvae that live in small pools of water which form in leaves of vegetation above ground.

Atrial chamber—the chamber surrounding the gill filaments between the gill slits and the spiracle.

Beaks—the keratinized structures sheathing the supralabial and infralabial cartilage in most tadpoles, except Orton Type 1 and 2.

BFA—see buccal floor arena.

BRA—see buccal roof arena.

Branchial food traps—regions of secretory mucosa covering the roof and the anterior wall of the filter cavities in most tadpoles. The traps usually cover the whole ventral surface of the ventral velum.

Buccal cavity—the internal portion of the mouth above the ceratohyal and the hypobranchial plate, anterior to the dorsal and ventral vela.

Buccal pockets—deep depressions in the buccal floor between the posterior margin of the ceratohyal and the anterior margin of the first ceratobranchial (= first gill cleft).

Buccal slits—perforations of the buccal pocket (first gill cleft) which connect the buccal cavity to the atrial chamber.

Buccal floor arena (BFA)—a large, circumscribed area in the center of the buccal floor.

Buccal floor arena papillae (BFA papillae)—rows of papillae that define the BFA.

Buccal roof arena (BRA)—defined area on the buccal roof directly above the buccal floor arena.

Buccal roof arena papillae (BRA papillae)—papillae that circumscribe and thus define the buccal roof arena.

cb.—see ceratobranchials.

Ceratobranchials (cb.)—the cartilaginous, skeletal elements of the branchial baskets; the gill bars.

Ceratohyal—the major cartilaginous skeletal elements of the buccal floor in tadpoles.

Choanae—see internal nares.

Ciliary groove—a horizontal groove that runs in the posterior and lateral margin of the pharynx from the anterior, lateral corner of the ventral velum to the esophagus. It is covered with cilia that transport mucus and food particles to the esophagus.

Collecting organs—see crescentic organs.

Crescentic organs—small, isolated branchial food traps of crescentic shape that lie at the anterior limit of the filter cavities in microhylid and rhinophrynid larvae.

Denticle formulae—numerical expression of the number of rows of denticles above and below the oral orifice (e.g., two rows above, three rows below = a 2/3 denticle formula).

Denticles—keratinized structures arranged in transverse rows that surround the beaks of most tadpoles.

Dorsal velum—a transverse flap across the posterior part of the mouth that separates the roof of the buccal cavity from the roof of the pharynx; the dorsal continuation of the ventral velum (= posterior filter valve).

Esophageal funnel—the region where the pharynx narrows into the esophagus.

Filter canals—partially or fully covered passages between neighboring filter folds on the filter plates.

Filter chambers—sections of the branchial baskets bounded laterally and medially by the filter plates, superiorly by the ventral velum, and ventrally by the gill slits. There are three filter cavities on each side.

Filter crevices—small passageways between two neighboring side folds on a single filter row.

Filter folds—narrow rows of gill filters that run from dorsal to ventral down the filter plates.

Filter niches — open, multi-sided spaces between secondary and tertiary filter folds on filter canals.

Filter plates — vertically oriented plates of connective tissue that arise from the ceratobranchials, which support the gill filter folds.

Filter rows—see filter folds.

Filter ruffles—see filter folds.

Funnel-mouth tadpoles—any larva with an exceptionally large expanded oral disc that is directed anterior or anterodorsally. The oral disc in these forms is usually free of denticles.

Gill filters—ruffled, epithelial organs associated with the posterior surfaces of cb. 1, the anterior surfaces of cb. 4, and both the anterior and posterior surfaces of cb. 2 and 3.

Glandular zone—a transverse band of secretory membrane that covers the posterior portion of the buccal roof to the dorsal velum.

Glottis—longitudinal slit-like opening to the bronchi that lies on the midline between the anterior portions of the 4th ceratobranchials.

Hypobranchial plate—the cartilaginous skeletal element between the ceratobranchials and the ceratohyal. It supports the posterior portion of the buccal floor.

Infralabial papillae—the most anterior projections in the buccal cavity, which lie over the infralabial cartilage

and its articulation with Meckel's cartilage.

Internal nares—slit-like openings of the anterior buccal roof.

Laryngeal disc—the circular, tracheal outline surrounding the glottis.

Lateral ridge papillae—subsidiary projections that lie lateral to the median ridge on the buccal roof.

Lateral roof papillae—any small projections that lie in the midportion of the buccal roof lateral to the BRA papillae.

Lingual papillae—premetamorphic projections that occur on the tongue anlage.

Main filter fold—the large, central ruffle of each filter row.

Median notch—a notch in the middle of the ventral velum.

Median ridge—a transversely oriented ridge or epithelial flap that lies in the midline of the buccal roof, approximately halfway between the upper beak and the dorsal velum.

Narial valve—extensive, free flaps of the posterior walls of the internal nares.

Narial valve projection—single, tall projections of the narial valve.

Opercular chamber—see atrial chamber.

Operculum—flap of skin arising from the hyoidean arch which covers the gill filaments.

Oral cavity—the region of the alimentary and respiratory system between the oral orifice anteriorly, the gill slits ventrally, and the esophagus posteriorly.

Oral disc—an expanded flap of skin surrounding the oral orifice. Denticle rows occur on the oral disc in most Orton Type 3 and 4 larvae.

Oral orifice—the entrance into the mouth or oral cavity.

Orton Type 1 Larvae—tadpoles that have paired spiracles, and lack keratinized mouth parts (Pipidae and Rhinophrynidae).

Orton Type 2 Larvae—tadpoles lacking keratinized mouth parts and having a single, medial spiracle (Microhylidae).

Orton Type 3 Larvae—tadpoles with keratinized mouth parts and a medial

spiracle (Ascaphidae and Discoglossidae).

Orton Type 4 Larvae—tadpoles having keratinized mouth parts and a single, sinistral spiracle (all families except those listed under Orton Types 1-3).

Pharyngeal by-pass—see buccal slits.

Pharyngeal cavity—the region of the oral cavity that lies between the dorsal and ventral vela anteriorly and the esophagus posteriorly. It is bounded ventrally by the pharyngeal gill slits.

Pond larvae, typical—tadpoles such as *Hyla regilla* and *Acris crepitans* which have a 2/3 denticle formula, live in small or medium-size ponds, and feed on suspended particles in the water column and graze on the substrate.

Posterior filter valve—see dorsal velum.

Postnarial arena—the region of the buccal roof between the nares anteriorly and the transverse median ridge posteriorly.

Postnarial papillae—papillae between the internal nares and the median ridge. These are usually in distinct, obliquely oriented rows from anteromedial to posterolateral behind the narial valve.

Postnarial ridges—epithelial folds in the postnarial arena.

Prenarial arena—the region of the buccal roof between the supralabial cartilages anteriorly and the internal nares posteriorly.

Prenarial papillae—see anterior narial papillae.

Prepocket papillae—papillae of the buccal floor that lie over the body of the ceratohyal anterior to the buccal pocket.

Pressure cushions—loose folds of epithelium descending from the roof of the pharynx posterior to the dorsal velum. There are usually two pressure cushions on each side of the pharynx.

Secretory pits—clusters of secretory cells that open in distinct pits along the posterior margin of the ventral velum and the glandular zone of the buccal roof.

Secretory ridges — mucus-secreting ridges that cover the branchial food trap surfaces on the ventral side of the ventral velum in most tadpoles (see Wassersug and Rosenberg, 1979).

Secretory zone—the exposed regions of mucus cell apices in the bottom of secretory pits and at the top of secretory ridges.

Side folds—secondary and tertiary branching patterns of the gill filters of each filter row.

Spicules—cartilaginous supports for the free, posterior surface of the ventral velum.

Spiracle—the opening in the operculum where water is expelled from the atrial chamber.

Suctorial tadpoles—larvae with an enlarged, oral disc used to adhere to substrate often in lotic environments.

Tongue anlage — the embryonic tongue pad that develops in the anterior portion of the buccal floor.

Ventral velum—a distinctive, movable (but nonmuscular) flap arising from the floor of the buccal cavity; it is attached anteriorly to the branchial baskets and to the superior margins of the filter plates (= anterior filter valve).

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